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A MULTI-SCALE INVESTIGATION OF FACTORS LIMITING
BULL TROUT VIABILITY

by

Tracy E. Bowerman

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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Logan, Utah

2013

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ABSTRACT

A Multi-scale Investigation of Factors Limiting
Bull Trout Viability

by

Tracy E. Bowerman, Doctor of Philosophy
Utah State University, 2013

Major Professor: Phaedra Budy
Department: Watershed Sciences

Effective conservation strategies for imperiled species require an understanding of processes that influence fitness throughout the organism's life cycle and across the range of habitats needed to complete that cycle. I evaluated factors that affect population viability of bull trout *Salvelinus confluentus*, a threatened freshwater char species, throughout individual life stages and over the entire life cycle.

I assessed the relationship between bull trout egg incubation success and environmental variables. Egg survival was negatively related to the percent of fine sediment in redds and positively related to hydraulic conductivity and the strength of downwelling. Next, I quantified juvenile bull trout survival rates and described movement patterns for this life stage. Juvenile bull trout emigrated from natal headwaters into larger rivers throughout the entire year and across a range of sizes. Estimates of juvenile survival rates improved dramatically when emigration was incorporated into the analysis.

I integrated my observations of bull trout survival, growth, and movement to create a life-cycle model, which I used to better understand how populations respond to changes in specific demographic rates. Bull trout populations were particularly sensitive to changes in juvenile growth and survival. The relative effect of changes to fertility rates and adult survival varied depending upon whether a population was composed primarily of large, migratory, or smaller, resident individuals. Dispersal helped to lower the probability of extinction for small or declining populations when neighboring populations were stable.

My research demonstrates that bull trout require access to habitats throughout entire watersheds to maintain population viability. My results suggest that limiting anthropogenic sources of fine sediment and maintaining areas of channel complexity that promote downwelling can be important for bull trout embryo survival. Management decisions should also consider the diverse behavior of juvenile bull trout and the wide range of habitat they use. Additionally, connectivity between populations is likely to be important for declining populations to persist. The diversity of life-history strategies expressed by bull trout helps maintain demographic stability within and among populations. As such, preservation of habitat integrity and full life-history diversity is imperative for conservation and recovery of bull trout populations range-wide.

(208 pages)

PUBLIC ABSTRACT

A Multi-scale Investigation of Factors Limiting
Bull Trout Viability

by

Tracy E. Bowerman, Doctor of Philosophy
Utah State University, 2013

Recent declines in many species of aquatic organisms have raised concerns about loss of biodiversity in river systems and the need to protect populations in peril. To conserve endangered species, scientists need to know information about the habitats organisms use throughout their life cycle and how environmental stressors cause populations to grow or decline. The goal of this research was to improve our understanding of the life-cycle requirements for bull trout (*Salvelinus confluentus*), a threatened freshwater fish species. I assessed environmental factors that affect bull trout egg incubation success and quantified juvenile bull trout movement patterns and survival rates. I then integrated this information into a life-cycle model that I used to evaluate how populations might respond to changes in survival, growth, reproduction, or migration rates, as a result of management actions, environmental variability, or climate change.

Bull trout egg survival was much lower in stream incubation environments with high amounts of fine sediment compared with environments with less fine sediment. High rates of downwelling, a process that drives surface water into the gravel, appeared

to improve egg survival rates. Juvenile bull trout demonstrated diverse movement patterns, and I was able to better estimate survival rates for this size class by accounting for movement out of the study area. Changes in juvenile survival rates and the time it took for individuals to mature had the largest influence on overall population trend. Bull trout populations that were composed of individuals that spawned earlier in their life cycle and grew more slowly were more vulnerable to changes in reproductive success (e.g., egg survival). In contrast, populations composed of late-maturing individuals that grew to larger sizes were more vulnerable to changes in adult survival rates (e.g., via harvest or predation). The potential for individuals to disperse, or move from one population into another to reproduce, was important to sustain declining populations when neighboring populations were stable. Collectively, this research demonstrates that bull trout require access to habitats throughout entire watersheds to maintain all components of their complex life cycles. Diversity in life-history traits, such as variation in age at maturation and migratory behavior, is important to help populations recover from environmental catastrophes and to persist in a changing environment.

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CHAPTER 1

INTRODUCTION

Biological diversity is the product of evolutionary forces operating over long time periods and across a range of scales, from individual genetic variation to variation in the composition and function of entire ecosystems. At a species level, populations are continually shaped by selective pressures in heterogeneous environments, and within-species diversity allows for genetic, behavioral, and demographic responses to changes in selective forces (Begon et al. 2006). Diversity in individual phenotypes and behavior, life-history strategies, and spatial distributions all help stabilize populations in highly variable environments and allow populations to adapt to evolutionary pressures (Gross 1991). However, when environmental change occurs rapidly, the rate of change can outpace the ability of a species to evolve concurrently (Carroll 2008). In altered or novel environments, adaptations that previously conferred a fitness advantage may become disadvantageous. Such maladaptations have been referred to as “evolutionary traps,” because environmental cues become decoupled from resulting fitness consequences (Schlaepfer et al. 2002; Fletcher et al. 2012).

Evolutionary traps can occur at almost any stage in an organism’s life history when formerly beneficial behavior leads to lower fitness in an altered environment. Examples of evolutionary traps include the choice of poor-quality habitats based on cues that previously correlated with high-quality habitat (Fletcher et al. 2012), mating with introduced species that results in infertile or low-fitness hybrid offspring (Kanda et al. 2002), and long-distance salmon spawning migrations that formerly allowed access to abundant resources, but now result in high mortality associated with dams (Lichatowich

2001). Such disconnects can occur at nearly any linkage between demographic, evolutionary, and physical templates, and have become more frequent as a result of anthropogenic habitat alterations. In light of the rapid rate of environmental changes occurring around the world, recovery of imperiled species will require a comprehensive understanding of the relationship between life-history adaptations and selective forces, and how changes in these forces affect population and evolutionary dynamics.

For organisms with complex life cycles, effective conservation planning should include evaluation of the interaction between demographic responses and environmental factors across multiple spatial and temporal scales (Lande 1988). Studies conducted at the scale of single habitat units and over a few years provide only a snapshot of ecological processes, and often focus on a single life stage or demographic rate. Research at larger spatial and temporal scales can provide a more comprehensive framework for understanding the linkages between individual life stages, physical habitat heterogeneity, and population demography, both within and among populations (Wiens 1989; Schlosser 1991).

A multi-scale approach that considers the heterogeneous riverscape is warranted for stream fishes, many of which use a variety of different habitats for spawning, feeding, and refugia during different life stages (Schlosser 1991; Fausch et al. 2002). The ability of stream fishes to escape poor environmental conditions, complete their life cycles, and maintain life-history diversity, depends upon the availability of critical habitats and the potential for fish to move among them (Fausch et al. 2002). Available resources and potential threats often vary along the longitudinal gradient of a stream, as do the resultant effects on population demographic rates such as survival and reproduction (Lowe et al.

2006). In many streams throughout the western United States, environmental threats and water quality impairments generally increase with stream order. Headwater streams may be affected by grazing, forest management, and wildfires, whereas lower portions of a watershed often face additional threats including channelization, urban development, decreased seasonal stream flow, and barriers to fish migration. This pattern can be depicted with a simple schematic (Figure 1.1), placed in the framework of the dynamic landscape model of stream fish population ecology described by Schlosser (1991). This diagram depicts the life cycle, habitat use, and common threats to bull trout *Salvelinus confluentus*, a threatened stream-dwelling salmonid.

Bull trout require cold, clean water and complex habitat (Buchanan and Gregory 1997; Baxter et al. 1999; Wissmar and Craig 2004), and as such, are considered an important indicator of aquatic ecosystem health. Throughout much of the species' range, bull trout populations have suffered declines as a result of direct fishing pressure, anthropogenic habitat alterations, introduction of non-native species, and barriers to migration (Fraley and Shepard 1989; McMahon et al. 2007; Parker et al. 2007). Bull trout populations are expected to be further affected by warming stream temperatures associated with climate change (Rieman et al. 2007; Isaak et al. 2010). In light of these threats, a thorough understanding of how environmental factors influence growth, movement, survival, and reproductive rates across a range of relevant spatial scales is necessary for managers to effectively prioritize conservation efforts and ultimately aid in the recovery of the species.

Bull trout exhibit variation in nearly every aspect of their life histories, a characteristic that complicates our ability to understand the full scope of factors limiting

populations. Bull trout have complex life cycles and exhibit multiple life-history strategies that often coexist, populations contain complex age structures and maturation schedules, and individuals often migrate long distances between habitats (Rieman and McIntyre 1993). Bull trout spawn during late summer through fall in headwater streams and tributaries (Rieman and McIntyre 1993; Ratliff et al. 1996). Females dig redds in areas with low stream gradient, small gravel substrate, proximity to cover, and often with groundwater influence (Fraley and Shepard 1989; Baxter and McPhail 1999; Baxter and Hauer 2000). Bull trout eggs develop throughout the fall, eggs hatch in midwinter, and alevins develop in the gravel until they have consumed their yolk sacs, after which they emerge as fry in early spring (Weaver and White 1985). Fry and juveniles rear in spawning habitat and adjacent headwater streams, where they are usually associated with the stream bottom (Goetz 1997; Sexauer and James 1997).

Bull trout populations are typically categorized into two distinct life-history strategies: resident and migratory (McPhail and Baxter 1996; Rieman and Allendorf 2001). The two forms often coexist, and in many populations, there may be no clear distinction between the two strategies, as individuals can exhibit both resident and migratory behavior during different portions of their life spans, and some populations show no genetic differentiation between the two life-history strategies (Homel et al. 2008). Resident bull trout may remain alongside juveniles in spawning habitats in the upper portions of a watershed for their entire life cycle, whereas migratory bull trout move downstream after one to four years to larger river systems and lakes that serve as migratory corridors and overwintering habitat (Fraley and Shepard 1989; Rieman and McIntyre 1993). Migratory adults typically spend several years in larger rivers (fluvial

life-history strategy), lakes (adfluvial life-history strategy), or the ocean (anadromous life-history strategy) before returning to natal streams to spawn (Fraley and Shepard 1989; Brenkman and Corbett 2005). Adult bull trout may move as far as 250 km between spawning grounds and overwintering habitat, but migration distances vary greatly among individuals and between years (McPhail and Baxter 1996; Hemmingsen et al. 2001). The suite of environmental factors most critical for bull trout growth, survival, and reproduction will vary depending upon life-history strategy and life stage. Thus, comprehensive management plans for bull trout should consider factors that affect bull trout survival on multiple spatial scales, ranging from individual spawning areas to entire large watersheds that include migratory corridors between habitats.

Despite a growing body of research on bull trout, there remains a paucity of information regarding factors limiting survival during egg development, fry emergence, and juvenile rearing, life stages during which mortality is naturally high, but also variable (Weaver and White 1985; Baxter and McPhail 1999; Williamson 2006). Previous bull trout population models have indicated that survival rates during early life stages can have large effects on the overall population growth rates (Rieman and McIntyre 1993; Al-Chokhachy 2006). In addition, population bottlenecks may occur during juvenile life stages, thereby regulating recruitment into adult age classes (Johnston et al. 2007). Thus, there is a need for research specific to egg, larval, and juvenile life stages to better understand specific habitat requirements and the effect of anthropogenic stressors on survival rates during this critical portion of the bull trout life cycle.

A second critical gap in our knowledge of bull trout is an understanding of the relationship between migration patterns and population demography. A great deal of

effort has put forth to describe seasonal migrations of bull trout in numerous populations (Swanberg 1997; DuPont et al. 2007; Monnot et al. 2008), but few studies have linked movement patterns to demographic rates such as survival or population growth. Bull trout demonstrate high natal and overwintering site fidelity (Swanberg 1997; Bahr and Shrimpton 2004; Watry and Scarnecchia 2008), although they exhibit substantial variation in migration distances and behavior among seasons (Bahr and Shrimpton 2004; Monnot et al. 2008). Numerous radio-telemetry studies have helped describe habitat use and distances moved over time, but larger inferences from movement patterns have been limited due to the relatively short time frames (usually 1 to 3 years) and small sample sizes (e.g., 6 to 70 individuals) of most studies (Swanberg 1997; Hogen and Scarnecchia 2006; DuPont et al. 2007). Additionally, rates of dispersal, or the movement of reproductive adults from one natal habitat to reproduce in another, have not been documented (Dunham and Rieman 1999).

The rate at which bull trout disperse between populations may have important implications for the persistence of metapopulations at the basin scale. A metapopulation can be broadly defined as a complex of multiple local populations that occupy discrete habitat patches and interact via dispersal (Hanski and Gilpin 1991). Metapopulation theory suggests that regional populations that interact with one another can be more resilient to environmental variability than isolated populations (Hanski and Simberloff 1997). Patterns of bull trout occupancy in spawning habitat patches suggest a metapopulation structure, with bull trout occurrence related to physical habitat features such as spawning patch size and distance among patches (Dunham and Rieman 1999; Rieman and Dunham 2000). However, research has not yet been conducted to evaluate

patterns of dispersal, the relationship between dispersal and life-history variability, and the effect of dispersal on overall population and metapopulation persistence.

The primary purpose of my dissertation research was to address existing gaps in our understanding of bull trout demography, with particular consideration of the variability in life stages, life-history expression, and migratory behavior across spatial scales and over the entire life cycle. My research objectives were to: (1) assess factors affecting bull trout egg incubation success (Chapter 2), (2) quantify juvenile bull trout movement patterns and survival rates (Chapter 3), and (3) evaluate how differences in life-history expression and migratory behavior influence population persistence and metapopulation dynamics (Chapter 4).

In Chapter 2, I used in situ experiments at the scale of individual spawning sites to investigate the relationships between abiotic variables and survival of bull trout eggs and larvae. While in the gravel, embryos are vulnerable to a number of environmental influences, both natural and anthropogenic, including displacement by streambed scour, suffocation due to inadequate oxygen supply, or entombment by fine sediments (Chapman 1988; DeVries 1997; Greig et al. 2005). In this chapter, I evaluated the effects of numerous abiotic factors on bull trout egg and alevin survival and development, including fine sediment, dissolved oxygen concentrations, vertical hydraulic gradient, and sediment hydraulic conductivity within artificial redds. I also evaluated ways in which bull trout may enhance egg incubation success by selecting suitable locations to spawn, and altering ambient conditions within the gravel via redd construction. This research improves our understanding of how physical factors affect early life-stage survival, and

will help inform restoration activities in impaired streams and guide management actions aimed at improving bull trout rearing conditions.

In Chapter 3, I used capture-mark-recapture data to estimate survival and evaluate movement patterns for juvenile bull trout. Estimates of demographic parameters are extremely limited for juvenile life stages, and are complicated by the variability in migratory behavior of bull trout (Downs et al. 2006; Al-Chokhachy and Budy 2008). To overcome this complication, I used a high degree of sampling effort to estimate emigration from a natal spawning stream, and explicitly incorporated movement patterns into the survival analysis. I captured and marked fish in a natal spawning tributary, and recaptured marked individuals throughout the surrounding watershed. This component of my research provides new insights into juvenile bull trout migratory behavior, describes movement patterns throughout a stream system, and demonstrates the importance of including behavior (e.g., migration rates) in the analysis and quantification of vital rates. My results help illustrate the importance of evaluating stream fish behavior at multiple spatial scales. In addition, estimates of juvenile survival from this research will help provide a baseline for studies in more degraded systems or as vital rates change over time, and provide important estimates of juvenile-specific survival for stage-structured population models.

In Chapter 4, I assimilated information from the previous chapters with additional estimates of demographic parameters to develop a stage-structured population viability model for bull trout. I used this model to investigate potential effects of management actions and climate change on the overall population growth rates for different bull trout life-history types. I estimated dispersal rates from capture-mark-recapture data, and used

empirical estimates of vital rates, population size, and dispersal, to create a spatially realistic metapopulation model composed of three distinct bull trout populations within a river basin. I then used the model to evaluate the potential effects of dispersal rates, management actions, and climate change on the persistence of individual populations, and the metapopulation as a whole. Results from this research can serve as a tool with which to explore the effect of future management actions or environmental disturbances on bull trout populations. This component of my research also provides a framework with which to evaluate the dynamics of other metapopulations composed of different spatial arrangements, life-history types, or population sizes, and a means to assess the potential for selective forces to differentially affect specific life-history traits.

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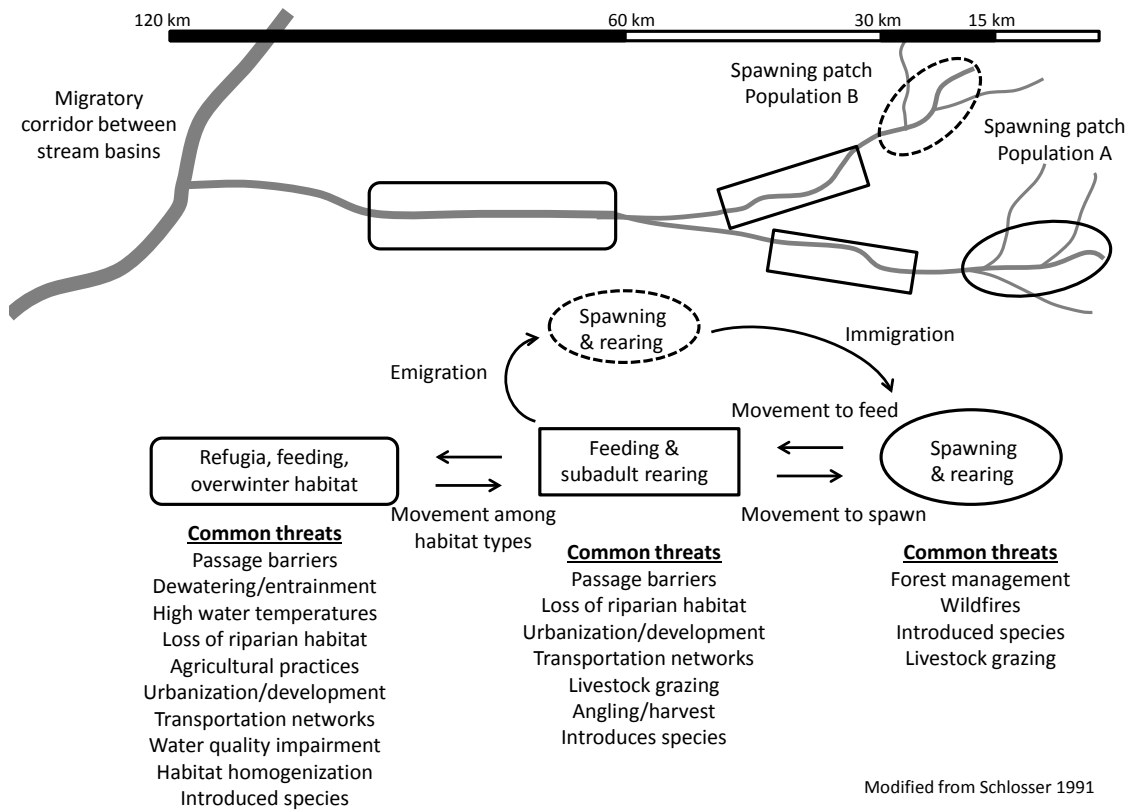


Figure 1.1. The basic life cycle of bull trout shown in relation to parts of a watershed used during various life stages, movement between habitats, the spatial scale at which such processes occur, and common threats associated with different portions of a stream system (sensu Schlosser 1991).

CHAPTER 2
EFFECTS OF FINE SEDIMENT, HYDRAULIC CONDUCTIVITY, AND
HYDRAULIC GRADIENT ON SURVIVAL AND DEVELOPMENT
OF BULL TROUT EMBRYOS¹

Abstract

A better understanding of how variability in the incubation environment affects embryo survival is important for the conservation of imperiled salmonid populations. However, relatively little is known about factors affecting egg survival rates for bull trout, a threatened char species. We conducted a field experiment to assess the relationship between site-specific environmental factors and bull trout embryo survival and emergence timing. We placed a known quantity of eggs in artificial redds and assessed water quality, hydraulic, and sedimentary characteristics within each redd throughout the development period. Survival of bull trout embryos was negatively related to percent fine sediment (<1mm) and positively related to downwelling, or negative rates of vertical hydraulic gradient. Fry also emerged earlier from redds with high percentages of fine sediment. Vertical hydraulic gradients were determined by the local bedform upon which redds were created, suggesting that placement of redds in locations with strong downwelling may enhance survival of bull trout embryos. Rates of dissolved oxygen and sediment hydraulic conductivity were significantly higher in redds compared with nearby undisturbed sediment, indicating that redd construction helped create a more favorable incubation environment with high hyporheic exchange capacity. Management actions that limit excess movement of fine sediment during spawning

¹ This chapter is co-authored by Tracy E. Bowerman, Bethany Neilson, and Phaedra Budy

seasons and preserve or restore areas of channel complexity that create vertical hydraulic gradients are critical for survival of bull trout at this sensitive life stage.

Introduction

Within the overall salmonid life cycle, a large but variable proportion of mortality occurs between the period of egg deposition and fry emergence (Quinn 2005). Salmonids construct redds by excavating a depression in the streambed gravel, in which the female lays her eggs. After the eggs are fertilized, she digs a second pit upstream of the first, allowing the current to carry gravel downstream to bury them. Eggs and larvae develop in this gravel environment, located within the saturated band of sediment surrounding alluvial rivers called the hyporheic zone, where groundwater and surface water mix (Stanford and Ward 1993). During development, embryos are susceptible to a number of disturbances which can cause mortality or reduce fitness, including displacement due to streambed scour, asphyxiation due to lack of oxygen or build-up of metabolic wastes (Greig 2007a), and entombment caused when fine sediment obstructs interstitial pathways, trapping fry in the gravel (Franssen et al. 2012). In turn, these factors that limit embryo survival and development are determined by physical characteristics of the spawning stream, attributes of the specific spawning location, and potentially, creation of the redd itself.

A great deal of research has focused on evaluating factors that affect survival of salmonid embryos because of the importance of this life stage to overall recruitment (see reviews in Chapman 1988; Bjornn and Reiser 1991; Groot and Margolis 1991). Common metrics associated with embryo survival and fitness include the composition of spawning sediments (Tappel and Bjornn 1983; Levasseur et al. 2006; Jensen et al. 2009),

intragravel flow velocities (Lapointe et al. 2004; Carling et al. 2006), and oxygen availability within the incubation environment (Chapman 1988; Greig et al. 2007a). These factors are interrelated, as fine sediment can reduce permeability, resulting in slower intragravel flows rates and reduced oxygen flux through the incubation environment (Rubin and Glimsater 1996). Lack of oxygen can lead to mortality via asphyxiation, or have sublethal effects such as reduced larval size and fitness (Sowden and Power 1985; Olsson and Persson 1986; Greig et al. 2007a). Fine sediment can also directly affect larval survival by blocking pathways through the gravel matrix and leading to entombment (Sear et al. 2008; Sternecker and Geist 2010; Franssen et al. 2012). In some locations, ambient levels of dissolved oxygen (DO) can be greatly reduced in hyporheic zones with strong groundwater influence, resulting in embryo mortality and impaired larval development even when fine sediment is limited (Malcolm et al. 2004; Youngson et al. 2004).

Characteristics of an individual redd location, and hence, spawning site selection, can also affect the quality of the incubation environment. The rate of intragravel (or hyporheic) flow is driven by variations in streambed pressure and sediment permeability across a range of spatial and temporal scales (Tonina and Buffington 2009a). At the scale of individual redds, variations in streambed pressure can result from changes in streambed elevation, flow depth, or velocity. For example, obstructions in the stream flow, including boulders, logs, gravel bars, and geomorphic bedforms (i.e., changes in streambed topography), such as pool-riffle transitions, create an area of high pressure upstream of the obstruction and a zone of low pressure on the downstream side. This differential drives stream water through the sediment, resulting in downwelling of stream

surface water on the upstream side and upwelling of hyporheic water on the downstream side of the obstruction (Thibodeaux and Boyle 1987; Tonina and Buffington 2007).

Downwelling surface water delivers dissolved oxygen into the sediment, whereas upwelling hyporheic water can have reduced DO as a result of oxygen consumption through biochemical processes in the sediment, particularly when hyporheic residence times are long (Boulton et al. 1998). Mixing with lower-oxygen groundwater can also contribute to chemically altered hyporheic water (Boulton et al. 1998; Hester and Gooseff 2010). At the channel scale, salmonids may select spawning locations in river segments with complex channel development, such as alluvial islands and side channels where strong hydraulic gradients have been observed (Geist 2000; Geist and Dauble 1998). At the spatial scale of the redd itself, some salmonid species appear to spawn at sites which exhibit strong localized downwelling and high rates of intragravel flow (Baxter and Hauer 2000; Coulombe-Pontbriand and Lapointe 2004).

Construction of a redd itself can alter local physical characteristics of the streambed in ways that may create more favorable intragravel conditions. First, redd excavation winnows away fine sediment, leaving a reduced proportion of fines relative to the original bed material (Kondolf et al. 1993), resulting in higher sediment permeability (Tonina and Buffington 2009b). Second, the topographic shape of a redd can generate a small-scale streambed feature, which has the potential to increase intragravel flow rates through the redd and thereby improve oxygen flux to developing eggs and larvae (Tonina and Buffington 2009b). However, the magnitude and significance of such spawning habitat alterations have not been tested under natural conditions.

Clearly, salmonid reproductive success depends upon a number of different physical factors that are regulated by geomorphic and hydraulic characteristics of a river system. Surface-groundwater interactions can determine baseline oxygen availability within the streambed sediment, whereas rates of intragravel flow and sediment composition vary spatially throughout the heterogeneous hyporheic zone, and can be altered by redd construction. Although multiple factors may be important in determining egg survival, most studies of salmonid incubation success focus on a single factor or process, and many use a single metric to describe the quality of spawning habitat. Such a singular focus may not accurately describe the numerous and complex processes affecting reproductive success.

Conservation planning for imperiled salmonid species, such as threatened bull trout *Salvelinus confluentus*, will benefit from a greater understanding of the relationship between baseline physical characteristics of a system and various factors that limit embryo survival and development. Embryo survival rates appear to be negatively related to the amount of fine sediment within the incubation environment (Weaver and White 1985), but relatively little information exists regarding egg and larval survival for bull trout, compared with other species of salmonids. Spawning areas for bull trout and closely related species have been associated with areas of large-scale groundwater upwelling (Curry and Noakes 1995; Baxter and Hauer 2000), and spawning success rates may be higher in locations with strong groundwater influence (Baxter and McPhail 1999). Observations of the association between bull trout and groundwater upwelling were based on measurements taken within a spawning reach, where groundwater influence may help moderate cold winter temperatures (Baxter and McPhail 1999).

However, at the scale of individual redds, bull trout often spawn on bedforms with localized downwelling, such as where the downstream edge of a pool merges into a riffle. In this study, we were particularly interested in investigating bull trout spawning success in relation hyporheic water quality and physical habitat characteristics measured at specific redd locations.

The goal of this study was to identify primary factors limiting survival rates and fitness of bull trout throughout the period of development in the gravel, and evaluate the processes controlling those factors. To meet this goal, our objectives were to measure survival of embryos to the time of hatch and to emergence, as well as the timing of fry emergence from the redd, in relation to the following abiotic factors: (i) intragravel water quality, including DO and pH, (ii) intragravel flow rates, and (iii) sediment composition. We measured these variables over time and across a range of natural habitats in three different spawning streams. We further evaluated whether these abiotic factors were influenced by: (i) the presence of chemically reduced groundwater, (ii) microhabitat characteristics that varied by individual redd location and therefore could be influenced by redd site selection, and (iii) the act of redd construction.

Materials and methods

Study Area

We conducted this study within the Metolius River basin, located on the east slope of the Cascade Mountains in central Oregon. The Metolius River flows approximately 45 km into Lake Billy Chinook, a 1,619 ha reservoir on the Deschutes River, a tributary to the Columbia River (Figure 2.1). The Metolius River system

contains a large population of fluvial and adfluvial bull trout. Adults reside primarily in the Metolius River and Lake Billy Chinook, and migrate upstream into smaller tributaries to spawn during September through October (Ratliff et al. 1996). Bull trout eggs hatch in mid-winter, and fry emerge from the gravel in late winter through early spring (Weeber et al. 2010).

We implemented this research on three spawning tributaries within the Metolius River system: Jack, Canyon, and Jefferson creeks (Figure 2.1). We selected these field sites to encompass a range of geomorphic and hydrologic characteristics representative of typical bull trout spawning habitat, including variation in groundwater inputs and sediment composition (Table 2.1). The 0.75 km portion of Jack Creek used in this study was characterized by a wide, shallow channel dissected by numerous fallen logs and islands, and a relatively uniform streambed of spawning-sized gravel. The 1.5 km long Canyon Creek study area was dominated by pool-riffle habitat with coarse cobble substrate and large patches of suitable spawning gravels. The 1 km long Jefferson Creek study area was laterally confined, with large pools, numerous log jams and fallen trees, and mobile sediment composed of well-sorted particles. We measured stage-height at the downstream end of each study area to monitor relative changes in discharge throughout the study period.

Construction of artificial redds

To assess conditions within the hyporheic environment during egg development, we created artificial redds in locations that exhibited habitat characteristics within the range of those typically used by bull trout in the Metolius River and similar systems (supplementary material Appendix A Table A.1). In each of the three study areas, we

selected 20 potential locations for redd placement based on spawning habitat characteristics described in previous studies, including gravel size (4 to 64 mm), water depth and velocity, and distance to cover (Goetz 1989; McCollister 1994; Weeber 2007). To minimize potential researcher bias, we then arbitrarily selected 10 of the 20 possible locations in each stream for artificial redd placement. Henceforth, we refer to these locations as "spawning sites", a term which is meant to describe the patch of spawning-sized gravel, suitable water depth and velocity, and the local bedform (e.g., pool-riffle transition) where redds were created (see Figure 2.2).

On September 19, 2009, we collected gametes from six female and two male bull trout. We produced two different parent crosses by fertilizing a mixture of eggs from three females with milt from both males combined. We mixed eggs and milt from multiple individuals so that failure of a single individual's gametes would not compromise the results, and we used two different parent crosses to minimize the potential for diseased eggs to contaminate the entire experiment. We allowed fertilized eggs to water harden for one hour before transporting them to artificial redds. We retained two batches of eggs from each parent cross in mesh trays in an outdoor hatchery incubator to assess fertilization success and survival rates under controlled conditions.

At each selected spawning site, we tried to replicate the morphological and sedimentological features of a natural bull trout redd (e.g., Greig et al. 2007b). For each artificial redd, we randomly selected one of the two parent crosses, and distributed 200 eggs amidst gravel within a 20 x 10 cm cylindrical incubation capsule made from a PVC frame with mesh sides and end caps (Figure 2.2). The size of mesh (2 x 1.5 mm) allowed water to flow through the capsules, but prevented escape of larval bull trout. We filled

incubation capsules with gravel excavated from the redd and truncated at 8 mm diameter to simulate the low amounts of fine sediment typically found within the egg pocket of a redd (Kondolf and Wolman 1993; Kondolf et al. 1993; Greig et al. 2007b). We placed two incubation capsules within the center of each pit and covered them with sediment by digging a second pit directly upstream of the first, sweeping gravel downstream to cover the incubation capsules in a manner that mimicked a spawning bull trout. Eggs were buried approximately 20 cm deep, a burial depth previously recorded for bull trout (DeVries 1997; Weeber et al. 2010). After completion, the tops of the incubation capsules were approximately 10 cm below the sediment surface.

During redd construction, we also installed one minipiezometer and a temperature sensor within each redd to measure intragravel water quality and temperature, and hydraulic characteristics (Figure 2.2). Minipiezometers were designed and installed according to methods described by Baxter et al. (2003), with the following adaptations: we used 1/2 inch PCV pipe with a perforated length of 10 cm, and we placed a screen around perforations to inhibit infiltration of fine sediment. The minipiezometer was placed between the two incubation capsules, with the middle of the screened portion located at egg burial depth. We attached two temperature sensors to a piece of rebar, with one buried 20 cm below the gravel surface to measure thermal conditions surrounding eggs, and the second sensor above the gravel to measure surface water temperatures. Sensors recorded water temperatures at hourly intervals throughout the study period. We used in-redd temperature measurements to determine degree days, calculated as the sum of daily mean water temperature above 0 °C during embryo development (Crisp 1988; Gould 1987). A second minipiezometer was inserted directly

into the sediment (Baxter et al. 2003), 20 cm deep and parallel to each redd (Figure 2.2). We used these "near-redd" measurements to describe properties of the hyporheic zone in undisturbed sediment within the same spawning site (0.2-0.8 m from the redd).

Survival and emergence timing

We determined natural variation in survival rates for both parent crosses based on eggs reared in the hatchery incubator. We removed one incubation capsule from each artificial redd in mid-January, after the predicted time of hatch based on degree days (Gould 1987; Weeber et al. 2010). We counted live larvae to determine survival to hatch (STH) in each redd. We also counted dead larvae and eggs to evaluate the stage of development at which mortality occurred.

At the time of hatch, we attached an emergence trap to the remaining incubation capsule in each redd to evaluate the time over which fry emerged and calculated survival to emergence (STE). The emergence trap consisted of a PVC elbow which locked onto the incubation capsule and was connected to a 1 m tube of heavy tarpaulin material with a PVC trap on the opposite end. The trap was fitted with a funnel, so that once fry had entered it, they could not swim back out (Figure 2.2). After fry began to emerge at the end of February, we counted emergent fry every two days, and calculated the timing and rate of emergence in relation to degree days. We removed incubation capsules after emergence was not observed for four or more days, and counted live fry that remained in incubation capsules at that time. We also counted dead fry and eggs and evaluated the stage of development when mortality occurred. We retained all sediment from incubation capsules for analysis, as described below.

Water quality, hydraulic, and sedimentary characteristics of redds

At each redd location, we measured physical factors that could potentially affect bull trout embryo survival and emergence timing. We assessed hyporheic water quality and intragravel flow metrics on five sampling occasions throughout the egg and larval development period (Figure 2.3). We measured intragravel water quality from the minipiezometers located in each redd. To sample water from a minipiezometer, we cleared the well of standing water, allowed it to re-fill, and then withdrew hyporheic water into a 150 mL syringe via a length of tubing. After withdrawing a water sample, we placed a multiprobe (YSI Model 556 MPS) directly into the syringe to measure DO ($\pm 0.1 \text{ mgL}^{-1}$), pH (± 0.1), and specific conductance ($\pm 0.1 \text{ }\mu\text{Scm}^{-1}$). We evaluated these metrics because low levels of DO and pH can have lethal effects on salmonid embryos (Daye and Garside 1977; Chapman 1988) and the presence of groundwater can affect DO and specific conductance (Malcolm et al. 2004).

To test for the presence of groundwater within redds, we compared measurements of water quality parameters taken from: (i) within the redd (termed in-redd hyporheic water), (ii) flowing water above the substrate surface (surface water), and (iii) water samples taken from the undisturbed spawning-sized sediment adjacent to the redd (near-redd hyporheic water). Intragravel water with reduced DO concentrations and increased specific conductance, compared with surface water, can be indicative of groundwater inputs or long hyporheic residence times (Malcolm et al. 2003; Malcolm et al. 2004; Tonina and Buffington 2009b). As such, reduced DO and higher specific conductance in near-redd hyporheic water would suggest longer hyporheic residence time or external

groundwater inputs, and higher DO and higher specific conductance of in-redd compared with near-redd hyporheic water would suggest that redd construction helped improve oxygen delivery through the redd (Tonina and Buffington 2009b).

We also measured water quality from within a subset of incubation capsules to evaluate whether water quality was altered directly in the egg pocket (egg-pocket water), either by the consumption of DO by embryos, which would reduce DO in the egg pocket relative to the surrounding gravels, or by accumulation of metabolic wastes, which could lower pH around the eggs. We sampled water from incubation capsules directly via a polyethelene tube, which extended from the egg pocket to the stream surface and attached to the syringe. We used the mutiprobe to measure pH, DO, and specific conductance.

On each sampling occasion, we also quantified the hydraulic conductivity and vertical hydraulic gradient within each redd as potential factors affecting survival. We compared these with the same measurements taken at the near-redd location to assess whether the variation in these factors was influenced primarily by characteristics of the spawning site or by redd creation. We used minipiezometers to assess vertical hydraulic gradient (VHG), a unitless measure that is positive under upwelling conditions and negative when downwelling is present. Following methods outlined in Baxter et al. (2003), we estimated VHG as $\Delta h / \Delta l$, where Δh is the difference in hydraulic head between water inside the piezometer and the stream surface (cm), and Δl is the depth of the screened opening below the substrate. To obtain Δh , we used a well sounder (Solinst model 101; accurate to 1 mm) to measure the water level inside the minipiezometer compared with the level of surface water. We performed falling head tests inside minipiezometers to estimate hydraulic conductivity (K), a measure of the capacity for a

porous medium to transmit subsurface flow (Tonina and Buffington 2009a). At many of our sites, water level equilibration occurred too quickly to perform repeated measurements, so we used a non-standard approach tested by Baxter et al. (2003) to estimate horizontal hydraulic conductivity (K_h) based on the equation

$$K_h = \left[\frac{(0.2501)(d_{\text{piezometer}})}{\Delta t} \right] \left[\log_e \frac{h_0}{h} \right],$$

where h_0 is the height of water in the piezometer at $t = 0$ (t_0), and h is the height of water in the piezometer at time t . Based on Darcy's Law, we estimated specific discharge (v) to approximate the rate of intragravel water flow through each redd. We assumed that vertical hydraulic conductivity values were 0.1 of horizontal values ($K_v = 0.1 \cdot K_h$; Baxter et al. 2003), and estimated v as $K_v \cdot VHG$. We also estimated oxygen flux through the redd post hoc based on $O_2\text{Flux} = DO \cdot \text{velocity} \cdot A_{\text{redd}}$, where A_{redd} is the area of the redd, and $\text{velocity} \approx \frac{v}{\text{porosity}}$ (Pinder and Celia 2006). Porosity was evaluated based on an approximation from Wu and Wang (2006).

We measured intragravel and surface water temperature at 15-minute intervals with high precision temperature sensors (HOBO Water Temp Pro v2; accuracy 0.2°C). We used two different metrics to describe temperature within the incubation environment. We recorded the minimum temperature experienced within each redd, because we hypothesized that near-freezing temperatures could be detrimental to eggs and larvae. We also calculated the average diel temperature variation at each site. We hypothesized that smaller diel temperature variations could signify either a more stable and potentially beneficial intragravel environment, or an environment with longer hyporheic flowpaths or groundwater influence, which could be detrimental to developing

embryos (Malcolm et al. 2004). However, due to an extremely high failure rate of sensors, temperature data were available for only 70% of artificial redds.

We estimated the depth of scour (mm) by placing a color-coded cable tie around the rebar at the top of the substrate on each sampling occasion. After removing rebar at the end of the study, we measured scour or fill based on the position of each cable tie relative to the original sediment height. We assessed sediment composition in each incubation capsule and from each redd after capsules had been removed. We used a modified McNeil sampler (Bunte and Abt 2001) to extract a sediment core from the area where the capsules were buried. We drove the sampler 20 cm into the gravel, and then transferred substrate from inside the sampler directly into a bucket. We extracted approximately 20 to 25 kg of sediment at each site. We air-dried, sieved and weighed particles >8mm diameter in the field, and oven-dried, mechanically sieved, and weighed smaller sediment sizes (<8 mm) in the lab (Bunte and Abt 2001). We classified sediment sizes based on the Wentworth scale, with a geometric progression of 15 size classes ranging from <0.25 to 90 mm (analyses were truncated at 90 mm). We determined cumulative particle size distributions from each redd, computed standard percentile values (e.g., D50; Bunte and Abt 2001), and calculated geometric means and Fredle index values (Lotspeich and Everest 1981). We dried and sieved all gravel from incubation boxes in the lab and determined sediment size distributions based on the same methods described above.

Statistical analyses

We determined baseline survival rates from eggs reared in the hatchery incubator, and evaluated whether there was a significant difference in survival between the two

parent crosses so we could account for potential sources of variation in further analyses. We used t-tests to compare survival rates between the parent crosses within the hatchery setting, as rearing conditions were the same for both groups. We analyzed differences in STH and STE between the two parent crosses in artificial redds with linear mixed effects models in the nlme package (Pinheiro et al. 2010) for the statistical software R 2.10. For this analysis, we modeled parent cross as a fixed effect, and the random effect of egg batch nested within study area.

We initiated assessment of the effects of abiotic redd variables on survival and emergence timing by first reducing the large number of potential predictor variables. Because we had repeated measurements of predictor variables (five sample periods) but only a single measure of survival response, we used minimum or maximum values if we expected extreme values could be limiting, otherwise we used the mean of measurements across sample periods. For each analysis described below, we used only a single sediment metric at a time, tested the fit the statistical model with each of the sediment metrics, and then retained the sediment metric that resulted in the best model fit in each analysis. The sediment indices we included were D_5 , D_{16} , D_{25} , Fredle Index, geometric mean, and the percent of sediment finer than 0.5 mm (PFT 0.5), percent finer than 1 mm (PFT 1), and the percent finer than 4 mm (PFT 4), measured in both redds (PFT_{redd}) and incubation capsules (PFT_{capsule}). Before running further analyses, we assessed multicollinearity between all remaining variables and did not include variables in the same model when correlations were greater than 0.7.

We used generalized mixed models (GLMM) with a binomial distribution (lme4 package in R 2.10; Crawley 2007; Bates et al. 2012) to assess the relationship between

response variables STH and STE and the following abiotic predictor variables, modeled as fixed effects: a sediment composition metric, VHG, K , v , scour, pH, DO, and specific conductance, scour, minimum temperature, and mean diel temperature range. We considered all abiotic factors individually as well as in combination, and included study area as a random effect in all models. We selected between competing models based on AICc. We considered models with $\Delta AICc < 2$ to have substantial support, $\Delta AICc$ values of > 4 to have considerably less support, and values > 10 to indicate that the model is unlikely (Burnham and Anderson 2002). We evaluated the models with the greatest support via examination of residuals.

We used multiple regression analysis to evaluate the relationship between emergence timing and abiotic conditions in each redd. We modeled the degree days at which the first 10% and 50% of fry that emerged from each artificial redd as response variables, and sediment composition, DO, pH, K , VHG, oxygen flux, and v as independent predictor variables. We considered all tests significant at $\alpha = 0.05$.

Last, we assessed whether observed variation in abiotic factors measured at individual redds could be attributed to the presence of low DO groundwater, individual spawning site characteristics, and redd construction. To assess potential changes in water quality parameters within the egg pocket as a result of oxygen consumption or metabolic waste accumulation, we used paired (dependent) t-tests to compare measurements of DO and pH from the egg pocket with in-redd water samples. To evaluate whether groundwater or redd creation affected water quality within redds, we fit linear mixed effects (LME) models with DO and pH as response variables, and water sample location and time plus an interaction treated as fixed effects, and sample period nested within redd

within study area as random effects. Water sample location was comprised of three categories: surface water, in-redd hyporheic water, and near-redd hyporheic water. To examine the effect of redd construction on K and VHG, we used linear mixed effects models with K and VHG as response variables, and modeled sample location with two categories (in-redd or near-redd) and time plus an interaction as fixed effects. We included sample period, redd, and study area as random effects in all models. We performed model selection based on a top-down approach (Zuur et al. 2009), compared models with likelihood ratio tests, and checked all residuals for normality.

Results

During the 2009-2010 period between redd creation and fry emergence, we observed notable differences in the degree of fluctuation in hydrology and temperature among the three study streams. Jack Creek was the most stable stream environment, with a nearly constant discharge and intragravel temperatures that varied between 2.08 and 5.99 °C (Figure 2.3). Canyon Creek experienced several spikes in the hydrograph in December and January as a result of rain events, and another from spring runoff, during the middle of the emergence period. The timing of high flow events in Jefferson Creek was similar to that of Canyon Creek, with two additional small peaks in the hydrograph in late October. Intragravel temperatures ranged from 1.57 to 7.95 °C in Canyon Creek and 1.73 to 7.59 °C in Jefferson Creek.

Embryo survival and emergence timing

Embryos reared in the controlled hatchery setting exhibited survival rates of 98% STH and 97% STE, demonstrating successful fertilization and very high survival rates

throughout embryo and larval development under controlled conditions. These results were similar to the highest survival rates observed in artificial redds (e.g., 97% STH and 95% STE), suggesting that some redd conditions were near-optimal. We observed no difference in survival between the parent crosses for eggs raised in the controlled hatchery setting (STH: $t = -0.2$, $df = 2$, $p = 0.86$; STE: $t = 0$, $df = 2$, $p = 1$). Likewise, we observed no significant difference in STH or STE between the two parent crosses in artificial redds (STH: $F = 0.01$, $df = 1, 2$, $p = 0.94$; STE: $F = 0.26$, $df = 1, 2$, $p = 0.66$). Therefore, we did not differentiate between parent crosses in subsequent analyses.

In general, survival to hatch was consistently high in Jack Creek and much more variable in Canyon and Jefferson creeks (Table 2.2). Across study streams, bull trout STH ranged between 3 and 97% ($66\% \pm 31$; mean \pm SD). Nearly all dead eggs had a visible embryo, indicating that mortality occurred partway through development. The two GLMM models with the greatest support based on AICc both included percent fine sediment and K as significant predictors of STH (Table 2.3). The addition of a third variable (VHG) did not improve model fit, so we present the results of the top-ranked model. Based on this model, STH was negatively related to $PFT1_{redd}$ and positively related to K (Table 2.4a). No interaction terms were significant.

When we removed incubation capsules after emergence, we found that in most capsules, a small number of fry (between 1 and 15) had not yet emerged, suggesting that we had slightly underrepresented the length of the emergence period. However, in two redds, a substantial number of live fry remained (96 and 115), even though emergence appeared to have stopped. In both of these redds, incubation capsules had relatively high amounts of fine sediment (7 and 13 $PFT1_{capsule}$, respectively). Both incubation capsules

also contained a relatively large number of dead larvae (13 and 30, respectively), compared with other capsules in which no more than 5 dead larvae were observed (dead larvae quickly decomposed and were eaten by aquatic macroinvertebrates). These observations suggest that these two incubation capsules had adequate intragravel conditions for some larvae to survive, but fine sediment may have prohibited their emergence. Here, we present the results of an analysis that includes survival of only bull trout larvae that emerged prior to the removal of incubation capsules because we could not be certain whether fry that remained in the gravel would have emerged on their own.

Survival to emergence was lower than STH at nearly all redd sites, ranging from 0 to 95% ($55\% \pm 36$). In general, STE was consistently higher in Jack Creek, the lowest and most variable in Jefferson Creek, and intermediate in Canyon Creek (Table 2.2). Based on AICc values, the two models that had considerable support both included significant effects of percent fine sediment in incubation capsules and VHG (Table 2.3). Once again, the addition of a third variable, K , did not improve the model, so we present the estimates from the top-ranking model (Table 2.4a). This model indicated that STE was negatively related to $PFT1_{\text{capsule}}$ and VHG. The negative coefficient associated with VHG indicates that survival is higher in redds that exhibit downwelling (a negative measure of VHG), and lower in redds that exhibit upwelling or very little vertical gradient. Once again, none of the interaction terms were significant.

Bull trout fry began to emerge on 26 February 2010 and continued over a period of 46 calendar days until incubation capsules were removed from the substrate after emergence had slowed or appeared to have stopped. Fry began emerging from redds between 620 and 700 degree days, and emergence peaked at 730-760 degree days (Figure

2.4). Based on the optimal linear regression model for the factors we tested, the number of degree days at which the first 10% of fry emerged from each redd was negatively related to percent fine sediment <0.5 mm in incubation capsules (Table 2.3b). We also detected a negative linear relationship between the timing of 50% of emergence and $PFT(0.5)_{\text{capsule}}$. Early emerging fry were shorter in length and had larger yolk sacs than those that emerged during the peak. Fry that emerged at 620-680 degree days had substantial amounts of yolk sac remaining and lacked parr marks, whereas most fry that emerged after 750 degree days had almost completely absorbed their yolk sacs and had fully developed parr markings.

Water quality, hydraulic, and sedimentary characteristics of redds

Water quality varied over time and among streams, but in general, in-redd hyporheic and egg-pocket water quality was more similar to surface than to near-redd hyporheic water. Concentrations of DO in water samples taken from the egg-pocket within incubation capsules ranged between 10.6 and 13.9 mg·L⁻¹. No significant difference occurred in any water chemistry attribute between in-redd and egg pocket hyporheic water (all $p > 0.05$; Table 2.4c), and as such, we did not detect any changes in DO or pH in egg pocket water samples as a result of embryo and larval consumption or excretion. For all water quality response variables analyzed with linear mixed models, there was a significant difference in measurements over time, but no significant difference in pH or specific conductance between surface, in-redd hyporheic, or near-redd hyporheic water sample locations (Figure 2.5; Table 2.4d). However, there was a significant difference in DO among sample locations (Table 2.4d). Dissolved oxygen concentrations in surface water varied between 10.2 and 14.7 mg·L⁻¹ (12.9 ± 0.87 ; mean

\pm SD) and were significantly higher than both in-redd and near-redd hyporheic water samples. Comparison between factors in the mixed effects model showed that surface water DO concentration were significantly higher than in-redd DO concentrations ($t = 2.91$, $df = 1, 56$, $p = 0.005$), where the lowest observed measurement was $8.31 \text{ mg}\cdot\text{L}^{-1}$ in a single redd, and all other measurements ranged between 10.1 and $13.9 \text{ mg}\cdot\text{L}^{-1}$ (12.5 ± 1.09). In-redd DO concentrations were, in turn, significantly higher than near-redd measurements ($t = -4.48$, $df = 1, 56$, $p < 0.001$), which varied between 2.0 and $14.2 \text{ mg}\cdot\text{L}^{-1}$ (11.3 ± 5.64).

At most spawning sites, estimates of sediment K were consistently higher than estimates from near-redd sediments, whereas VHGs were similar between in-redd and near-redd measurements (Figure 2.6). Rates of K varied between 0.10 and $0.55 \text{ cm}\cdot\text{sec}^{-1}$, and in-redd measurements were significantly higher than the near-redd measurements, where K ranged from 0.015 to $0.48 \text{ cm}\cdot\text{s}^{-1}$ (Table 2.4d). In contrast, rates of VHG were similar between in-redd and near-redd measurements, with the majority of sites exhibiting downwelling (i.e. negative VHG; Figure 6). Measurements of VHG varied between -0.15 and 0.075 in redds, and between -0.18 and 0.05 in near-redd locations.

Grain size distributions varied considerably among redds and streams, as did the sediment composition within incubation capsules. Cumulative percent fine sediment $< 1 \text{ mm}$ ranged between 0.4 and 38.8% (6.0 ± 9.4 ; mean \pm SD) in incubation capsules at hatch, from 0.1 to 40.3% in incubation capsules at emergence (9.8 ± 11.9), and from 6.8 to 33.5% in artificial redds (18.2 ± 6.2 ; Table 2.3). In Jack Creek, incubation capsules typically had low percent fines, often lower than the surrounding redd sediment. In contrast, the range of fine sediment accumulation in incubation capsules in both Canyon

and Jefferson Creeks was larger than that of the redd sediment in those systems. All incubation capsules that had high percentages of fines (more than 20% fine sediment <1 mm) were in locations where sufficient scour occurred to expose the tops of incubation capsules (7-9 cm; Table 2.2).

Discussion

Effects of VHG, and K, and fine sediment on bull trout survival and emergence timing

Within the range of conditions examined, our results demonstrated that survival rates of bull trout embryos were related to fine sediment, VHG, and *K*, and that a combination of these variables may have different effects on survival during distinct periods of early life-stage development. Percent fine sediment had clear effects on both survival and the timing of emergence from the redd, and we found that the percentage of fine sediment was a better predictor of both survival and emergence timing than were other metrics describing sediment composition (e.g., Fredle Index, geometric mean). A negative relationship between embryo survival and fine sediments in spawning gravels has been well-documented for many species of salmonids (Chapman 1988; Argent and Flebbe 1999; Fudge et al. 2008). In a meta-analysis based on 14 published datasets, Jensen et al. (2009) found that increasing amounts of fine sediments in stream substrates reduced egg-to-fry survival of four salmon species in both laboratory and field studies. Thus, general patterns exist between salmonid egg survival and fine sediment, irrespective of species or study stream.

Accumulation of fine sediments in the incubation environment can affect two of the primary mechanisms of egg and larval mortality. Fine sediment can reduce rates of

intragravel water flow through the incubation environment, causing asphyxiation from lack of oxygen or reducing the rate of metabolic waste removal (Greig et al. 2007b). Second, fine sediment can also prevent fry from escaping the gravel environment, resulting in entombment (Sear et al. 2008; Franssen et al. 2012). In this study, observations of dead eggs at the time of hatch, as well as the positive relationship between K and STH suggest that asphyxiation due to insufficient intragravel water flow may have been one cause of egg mortality. However, our data showed no clear relationship between DO measurements and survival or emergence timing. Greig et al. (2005, 2007b) also found that oxygen concentration alone was a poor predictor of survival and suggest that oxygen flux, a metric that combines oxygen concentration and intragravel water velocity, can be a better predictor of survival (Greig et al. 2007a). In this study, even though K was significantly related to STH, v (a measure of intragravel velocity that is a combined metric of K and VHG) was a poorer predictor of survival than the two measures considered separately. Thus, in our study, oxygen flux was also not one of the best predictors of survival.

We acknowledge that our understanding of oxygen availability may have been limited for several reasons. First, we measured DO concentrations at discrete intervals, and thus may not have captured variations in oxygen concentrations that can result from hydrologic events (Malcolm et al. 2006). Second, even in the absence of reduced oxygen concentrations, very fine sediment (e.g., clay-sized particles) can physically occlude pores on egg membranes, leading to asphyxiation (Greig et al. 2005). We visually observed very little organic material and clay-sized particles in gravel samples, although our study was not designed to test for such an effect. Additionally, oxygen availability

can vary among egg locations within a redd (Greig et al. 2007b) and although we measured DO directly in egg pockets, we did not sample at the spatial scale of individual eggs.

After hatch, developing larvae may move through gravel interstices to seek more favorable conditions, such as areas with increased oxygen availability (Bams 1967). However, infiltration of fine sediment may prevent larvae from moving to sufficient intragravel conditions or from escaping to the stream surface. We observed potential evidence of fine sediment impeding fry emergence from two incubation capsules, in which we found recently deceased fry entombed in fine sediment, and large numbers of live fry that had not yet emerged. In such cases, fine sediment may trap fry inside the redd, whereas in others, it may cause them to emerge prematurely, perhaps to escape sub-optimal environmental conditions (Phillips et al. 1975; Olsson and Persson 1986; Franssen et al. 2012). Some researchers have suggested that fry that emerge earlier may have a competitive advantage because they establish feeding territories (Einum and Fleming 2000). However, others hypothesize that larval fish that emerge prematurely with large yolk sacs may be poor swimmers and more susceptible to predation and downstream displacement than their fully-developed counterparts (Louhi et al. 2011). As such, conditions within the spawning environment may have sublethal effects on surviving fry, which may reduce fitness in later life stages (Roussel 2007; Skoglund et al. 2011).

Streambed scour was not a significant variable in any analyses, but may have indirectly affected embryo survival. At all locations where the percentage of fines in the incubation capsule was substantially greater than that of the surrounding redd, scour

exceeded 7 mm, and was sufficient for the top of the incubation capsule to be exposed at the streambed surface. We observed scour as a result of bull trout spawning on top of artificial redds, as well as after elevated flow events in Jefferson and Canyon creeks. In contrast, very little scour occurred in Jack Creek, where the hydrograph remained stable. Once capsules were exposed at the surface, the mesh size likely served to trap more fine sediment than would have remained in the egg pocket otherwise. The lack of similar infiltration in incubation capsules that remained covered suggests that the surface layer of gravel may help prevent the accumulation of fine sediment in the egg pocket (Meyer et al. 2005). Scour is often considered a potential threat to salmonid egg survival due to physical displacement of eggs. Our observations demonstrate that even when scour is insufficient to expose eggs, removal of the top layer of sediment may contribute to infiltration of fines into the egg pocket (Lisle 1989).

The importance of VHГ as a significant predictor of STE suggests that the rate of intragravel flow through the redd can help offset some of the negative effects of fine sediment. The potential for VHГ to help mitigate embryo mortality in substrates with moderate amounts of fine sediment has been suggested previously, although VHГ is unlikely to benefit survival when silt contents are high (Lapointe et al. 2004). Contrary to our findings, in a recent laboratory study, Franssen et al. (2012) did not find a significant effect of VHГ on survival to emergence of brook trout *Salvelinus fontinalis*, raised in laboratory incubators across a range of substrate compositions. We suggest that the heterogeneity of a dynamic stream environment could contribute to the difference in our results compared with those from a laboratory setting. In natural streams, there is substantial spatial and temporal variation in sediment sorting, stream discharge, and the

strength of VHG. We posit that in a natural stream, strong rates of downwelling, such as we observed, may help mitigate some of the negative effects of fine sediment. This could potentially occur either via driving oxygenated water into the redd, or by maintaining interstitial pathways through the gravel when intermediate amounts of fine sediment are present.

Influence of groundwater, site selection, and redd creation on incubation conditions

Differences in DO and K within redds compared with near-redd measurements taken in undisturbed sediment adjacent to redds indicate that redd construction altered sediment composition and arrangement to a degree that effectively enhanced the intragravel environment. Redd construction can increase K by winnowing away fine sediment and loosening compacted sediments (Montgomery et al. 1996; Zimmermann and Lapointe 2005), resulting in shorter hyporheic flowpaths, and higher DO concentrations (Tonina and Buffington 2007; Tonina and Buffington 2009b). However, even in undisturbed near-redd sediment, water quality attributes of pH and specific conductance were similar to that of in-redd and surface water. As such, we found no indication of groundwater inputs at the scale of individual redds, despite the spring-fed nature of the study streams. Although DO levels were lower in the near-redd water samples relative to in-redd and near-redd water, we only observed low DO concentrations (<8 mg/L) in a few spawning sites. These combined results suggest that variations in DO were likely the result of slightly longer hyporheic flow paths, but that at egg burial depth, the sediment in our study areas was generally dominated by surface water exchange.

Our data suggest that locations with strong downwelling can enhance incubation conditions, and accordingly, we would expect the choice of spawning location to affect

embryo survival rates. Many of the artificial redds were located in areas where hydraulic head gradients created downwelling conditions (e.g., bedforms at the transition between pool and riffle, or just upstream of a fallen log), where bull trout redds are often observed (e.g., Baxter and Hauer 2000). We detected no difference between VHG in redds compared to near-redd measurements, suggesting that if the shape of a redd does increase downwelling, as demonstrated by hydraulic models (Tonina and Buffington 2009b), either our measurement technique did not allow us to detect changes of this magnitude, or we did not measure VHG at the point of greatest downwelling. Rates of VHG varied among sites, and the largest rates of downwelling occurred at spawning sites located above steep riffles and log jams, each of which created a vertical step in the stream surface.

Conservation and management implications

Our results indicate that bull trout egg and larval survival rates are negatively related to the percentage of fine sediment in the spawning environment, but that localized downwelling at individual redd sites can potentially help mitigate the negative effect of fine sediment on survival. Our research suggests that spawning habitat indices based on a single variable, such as percent fine sediment or oxygen concentration alone, may not adequately characterize the complex processes that affect bull trout spawning success. Alteration to the streambed substrate through redd creation can increase hyporheic flow rates and thereby increase oxygen concentrations, resulting in a more favorable incubation environment. Spawning site location is also important, as transitional geomorphic bedforms and complex habitat, such as large woody debris, create areas of downwelling that may help mitigate the negative effect of fine sediment.

The variables that affect bull trout survival and larval development are in turn affected by larger geomorphic controls. High percentages of fine sediment in spawning gravels clearly have a negative effect on incubation success, but the mobility of fine sediment varies greatly between streams and seasons (Lisle 1989). Fine sediment loading can result from anthropogenic changes, such as logging, grazing, and road construction (Beschta 1978), and can also result from fires, landslides, and other natural disturbances. Some geologic landscapes are also inherently much higher in fines. Changing these larger drivers of sediment composition in spawning areas may take a long time, or may be beyond the scope of management. However, on a smaller temporal and spatial scale, managers have the capability to maintain and restore features that create hydraulic complexity, such as fallen wood and pool riffle sequences. Such features can create locations of high VHG, enhance the availability of spawning sites with strong downwelling, and potentially help mitigate the effects of fine sediment in the incubation environment.

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Table 2.1. Field site characteristics in each of three streams where artificial redds were placed. Percent fine sediment was calculated from subsurface volumetric subsampling prior to excavation of artificial redds, and dominant spawning habitat was estimated visually.

Descriptor	Jack Creek	Canyon Creek	Jefferson Creek
Drainage area (km ²)	33	69	73
Gradient (%) ^a	1.4	1.5	2.5
Baseflow discharge (m ³ ·s ⁻¹) ^{a,b} at watershed outlet	1.6	1.3	2.8
Mean width (m) ^b	18	8.5	7
Mean percent fine sediment <4 mm ^b	22	18	25
Dominant spawning habitat ^b	glide	pool tail	pool tail/riffle
Primary water source	spring-fed	springs/snowmelt	springs/snowmelt/ glacial melt

^aGoetz 1997

^bPilot research, this study

Table 2.2. Mean, range, and number of observations in each of the three study streams for two response variables, survival to hatch and survival to emergence, and predictor variables measured in each redd. Measurements of scour represent the depth of sediment lost from the surface of a redd; measurements of fill represent sediment deposited onto a redd, and are denoted by a + sign.

Variable measured	Jack Creek			Canyon Creek			Jefferson Creek		
	Mean	Range	n	Mean	Range	n	Mean	Range	n
Survival to hatch (%)	94	90 - 97	10	64	17 - 94	9	40	3 - 67	10
Survival to emergence (%)	87	65 - 95	10	51	3 - 89	9	27	0 - 77	10
% fines <1mm in redd	2.9	1.0 - 8.1	10	4.4	1.3 - 9.1	9	11.4	7.2 - 16.1	10
% fines <1mm in capsule at hatch	0.8	0.3 - 1.9	10	1.6	0.5 - 3.5	9	14.1	3.1 - 19.9	10
% fines <1mm in capsule at emergence	1	0.3 - 1.9	10	5.4	0.8 - 20.5	9	19.7	6.3 - 32.0	10
Scour/fill depth (mm)	1.5	0 - 6	10	3	0 - 7	9	3.2	+1 - 7	10

Table 2.3. Candidate models describing the relationship between abiotic independent variables and two response variables: survival to hatch (STH) and survival to emergence (STE). Number of parameters, Akaike's information criterion corrected for small sample (AIC_c), difference in AIC_c relative to the best model (ΔAIC_c) and log-likelihood are shown.

Fixed effects in GLMM	No. of parameters	AIC_c	ΔAIC_c	Log-likelihood
Survival to hatch (STH)				
$PFT1_{redd} + K$	5	128.24	0	-57.76
$PFT1_{redd} + K + VH_G$	6	129.17	0.93	-56.59
$PFT1_{capsule} + K$	5	130.82	2.58	-59.05
$PFT1_{redd}$	4	131.55	3.31	-60.91
K (average)	4	132.57	4.33	-61.42
$Fredle_{redd}$	4	132.7	4.46	-61.48
v (average)	4	133.57	5.33	-61.91
DO flux	4	133.76	5.52	-62.01
Geometric mean _{redd}	4	134.33	6.09	-62.29
VH_G	4	134.33	6.09	-62.3
DO (minimum)	4	136.97	8.73	-63.61
pH (average)	4	137.31	9.07	-63.79
Survival to emergence (STE)				
$PFT1_{capsule} + VH_G$	5	131.43	0	-59.29
$PFT1_{capsule} + VH_G + K$	6	133.07	1.63	-58.43
$PFT1_{capsule} + K$	5	134.56	3.12	-60.85
$PFT1_{capsule}$	4	135.92	4.49	-63.05
$PFT1_{redd}$	4	139.51	8.08	-64.85
K (minimum)	4	141.6	10.17	-65.89
DO flux	4	142.05	10.62	-66.12
v (average)	4	143.26	11.83	-66.72
VH_G (average)	4	143.54	12.11	-66.86
pH (average)	4	144.16	12.73	-67.17
DO (minimum)	4	145.91	14.48	-68.05

Table 2.4. Results from statistical tests used to analyze: (a) effects of abiotic factors on egg survival to hatch and to emergence based on generalized linear mixed effects model (GLMM), (b) effects of abiotic factors on fry emergence timing, (c) water quality variables in egg pocket water compared with in-redd water, and (d) differences in water quality and physical variables among sample locations in mixed effects models.

(a) GLMM to assess survival

Response	Parameter	Estimate	SE	df	z-stat	p-val
Survival to hatch	Intercept	-1.93	1.63	24	-1.18	0.23
	PFT _{redd} <1mm	-0.17	0.06		-2.98	<0.01
	K	10.14	3.71		2.73	<0.01
Survival to emergence	Intercept	0.46	0.41	23	1.12	0.27
	PFT _{capsule} <1mm	-0.15	0.03		-5.55	<0.01
	VHG	-25.04	8.49		-2.95	<0.01

(b) Linear regression to assess emergence timing

Response	Parameter	Estimate	SE	df	t-stat	p-val
10% of emergence	Intercept	738.08	7.06	25	104.59	<0.01
	PFT _{capsule} <0.5mm	-4.92	0.84		-5.86	<0.01
50% emergence	Intercept	759.91	6.31	25	120.49	<0.01
	PFT _{capsule} <0.5mm	-8.02	1.49		-5.40	<0.01

(c) Paired (dependent) t-test of egg pocket vs. in-redd water

Variable of interest	df	t-stat	p-val
specific conductivity	20	-0.77	0.45
DO (mg·L ⁻¹)	20	0.42	0.68
pH	20	0.17	0.87

(d) Type III tests of fixed effects for hydraulic and water quality measurements

Response variable	Parameter	df(num)	df(den)	F-stat	p-val
pH	Sample location	2	58	1.08	0.35
	Time	4	356	90.18	<0.01
Specific conductance	Sample location	2	58	1.43	0.25
	Time	4	356	40.24	<0.01
DO (mg·L ⁻¹)	Sample location	2	56	27.70	<0.01
	Time	4	344	118.74	<0.01
K (cm·s ⁻¹)	Sample location	1	28	49.25	<0.01
	Time	4	224	3.49	0.01
	Sample location * Time	4	224	3.09	0.02
VHG	Sample location	1	28	1.13	0.30
	Time	4	228	4.81	<0.01

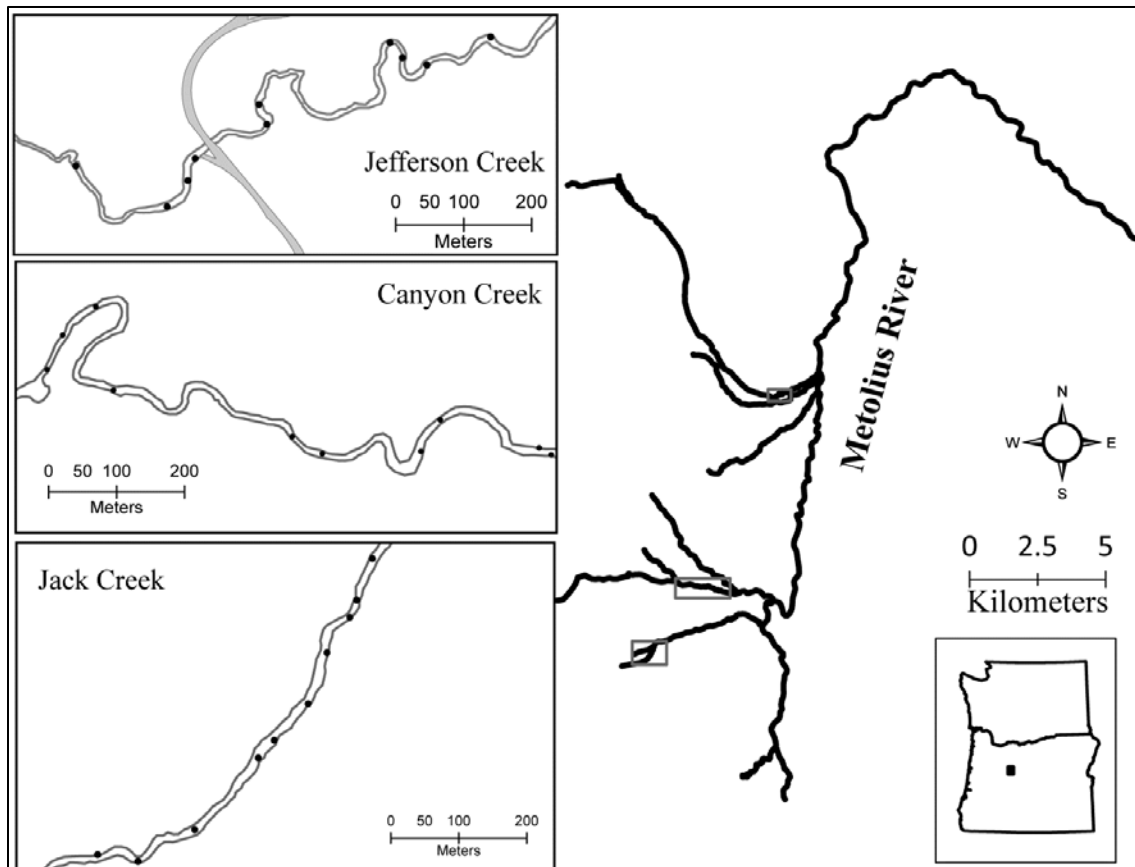


Figure 2.1. Map of the Metolius River, Oregon, showing study areas in three different streams: Jack, Canyon, and Jefferson creeks. Insets show the location of artificial redds (black dots) within each study area.

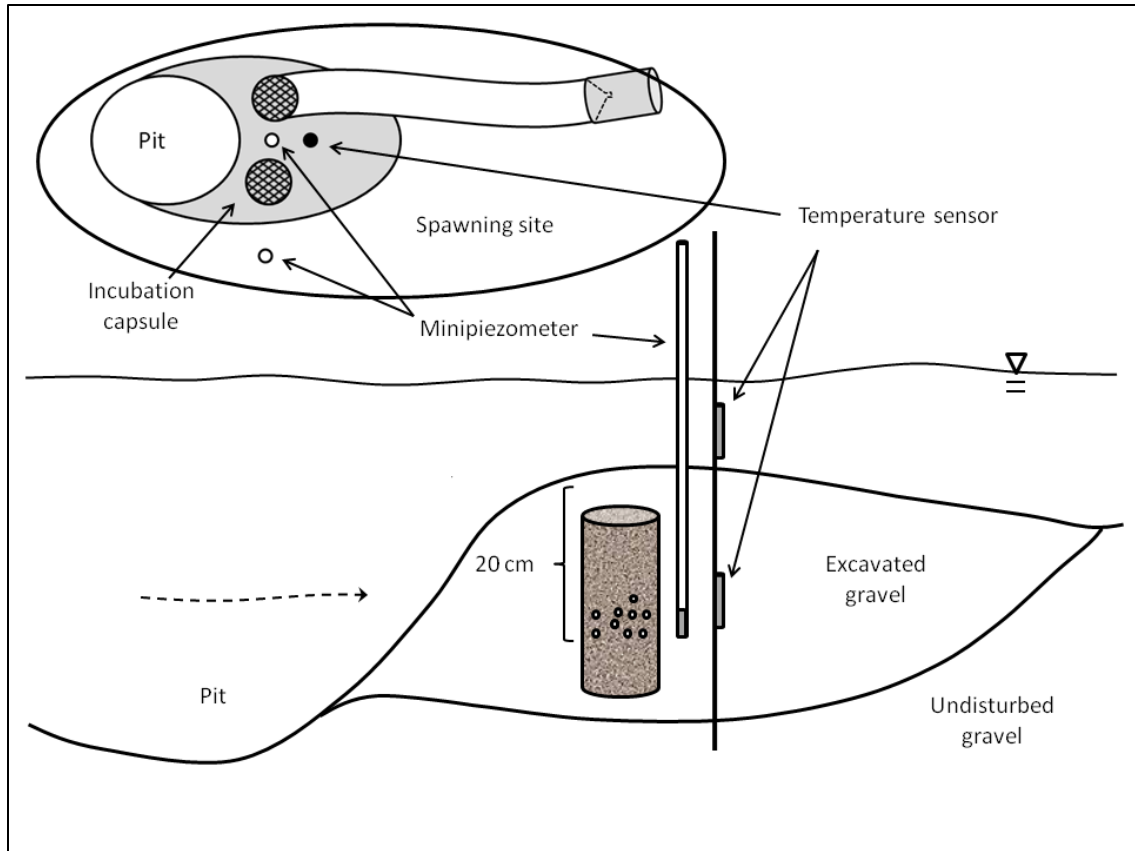


Figure 2.2. Schematic of artificial redd showing the location of incubation capsule, minipiezometer and temperature sensors located within the excavated substrate (in-redd measurement location). Plan view (inset) depicts the area of suitable spawning gravel at a spawning site, and the location of sampling equipment within the redd, as well as the minipiezometer located in spawning-sized substrate outside of the redd (near-redd measurements), and the design of an emergence trap.

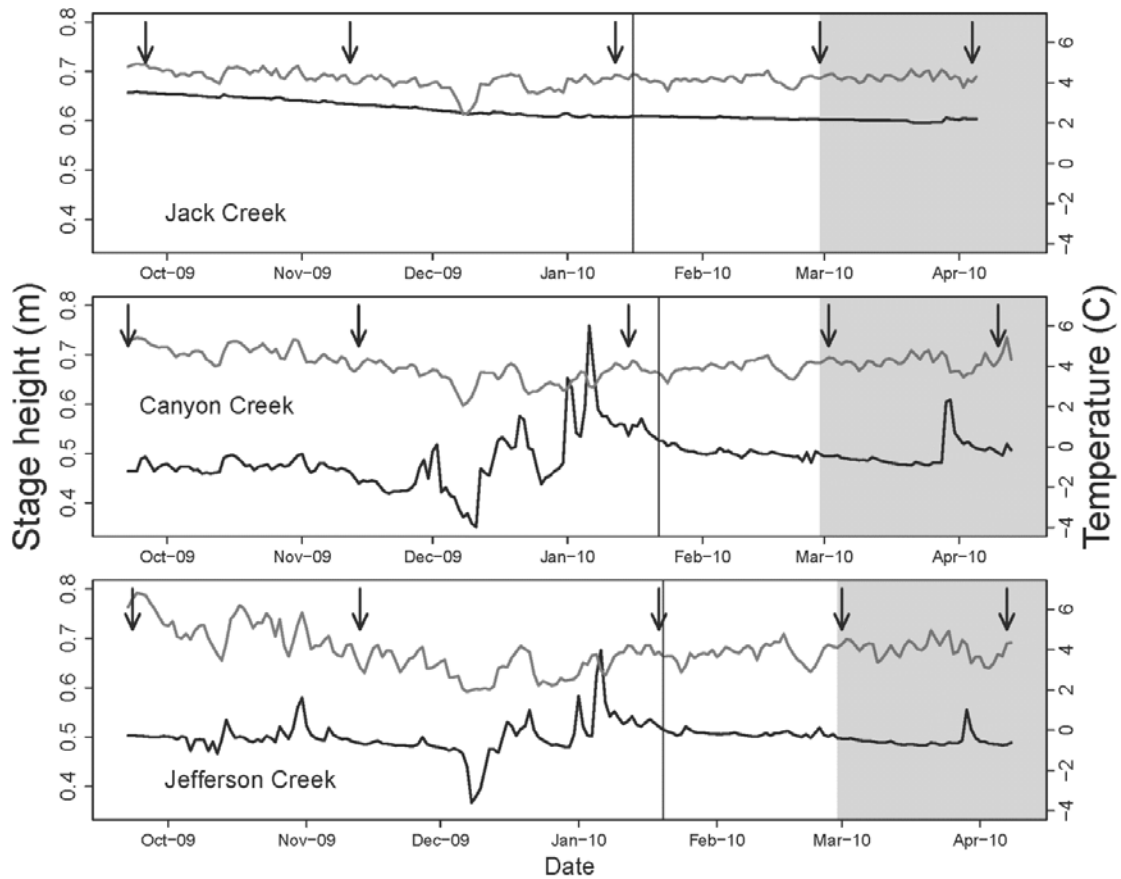


Figure 2.3. Discharge (black line), shown as stage height above an arbitrary datum, for the three study areas. Temperature (gray line) is shown on the second y-axis. Arrows mark the timing of each of the five sampling occasion. The vertical black line represents the time when one incubation capsule was removed from each redd and STH assessed, and the duration of emergence is shaded in light gray.

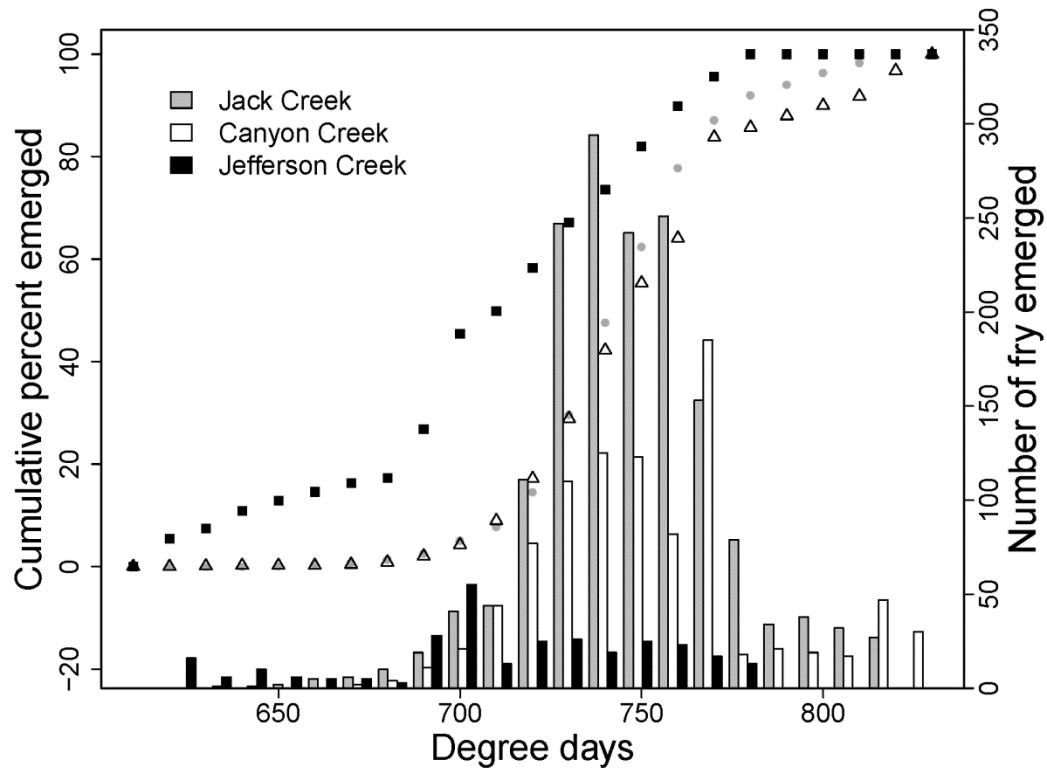


Figure 2.4. Cumulative percent of total emerging fry per degree day (gray dots = fry emerging from Jack Creek redds, open triangles = Canyon Creek redds, black squares = Jefferson Creek redds). The second y-axis shows the total number of fry that emerged from all redds in each stream per degree day (gray bars = Jack Creek redds, open bars = Canyon Creek redds, black bars = Jefferson Creek redds). Degree day was calculated as the sum of daily mean water temperature above 0 °C during embryo development.

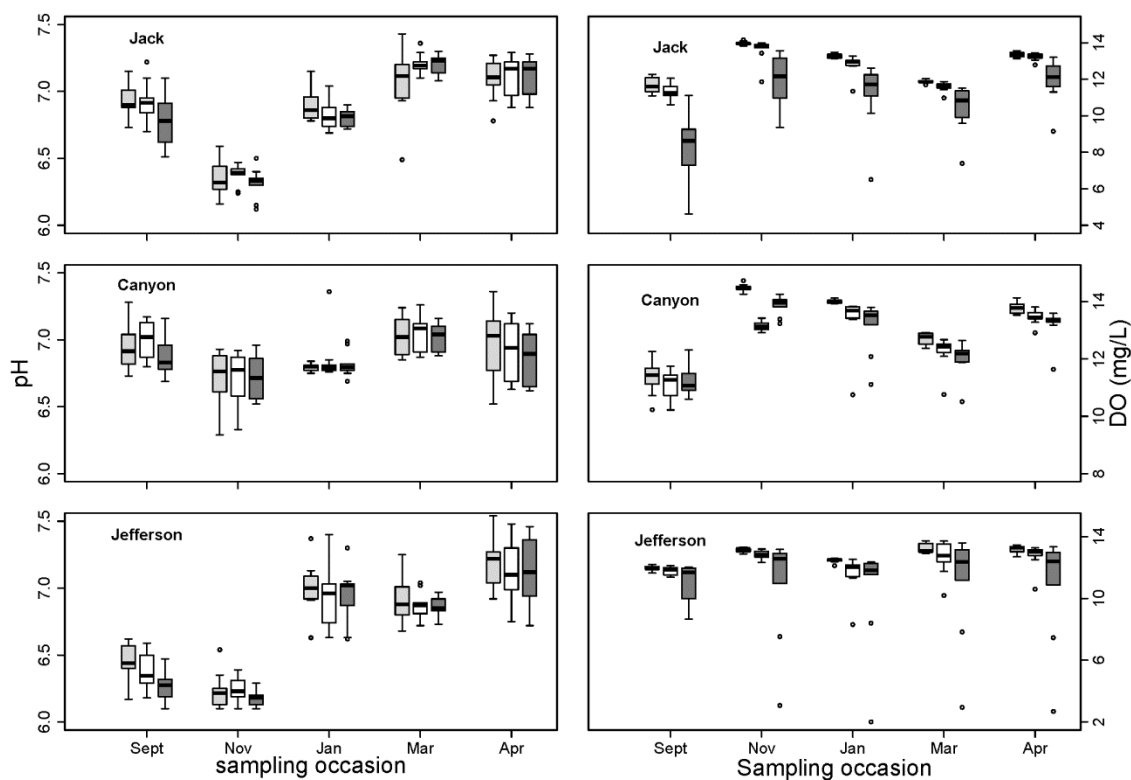


Figure 2.5. Measurements of pH (left panel) and dissolved oxygen concentration (DO; $\text{mg} \cdot \text{L}^{-1}$; right panel) in each of the three study areas for water samples taken from in-redd hyporheic water (open boxes), near-redd hyporheic water (light gray boxes), and surface water (dark gray boxes). Boxes represent the upper and lower quartiles, the mid-line represents the median value, whiskers depict the maximum and minimum values, and outliers are shown by dots.

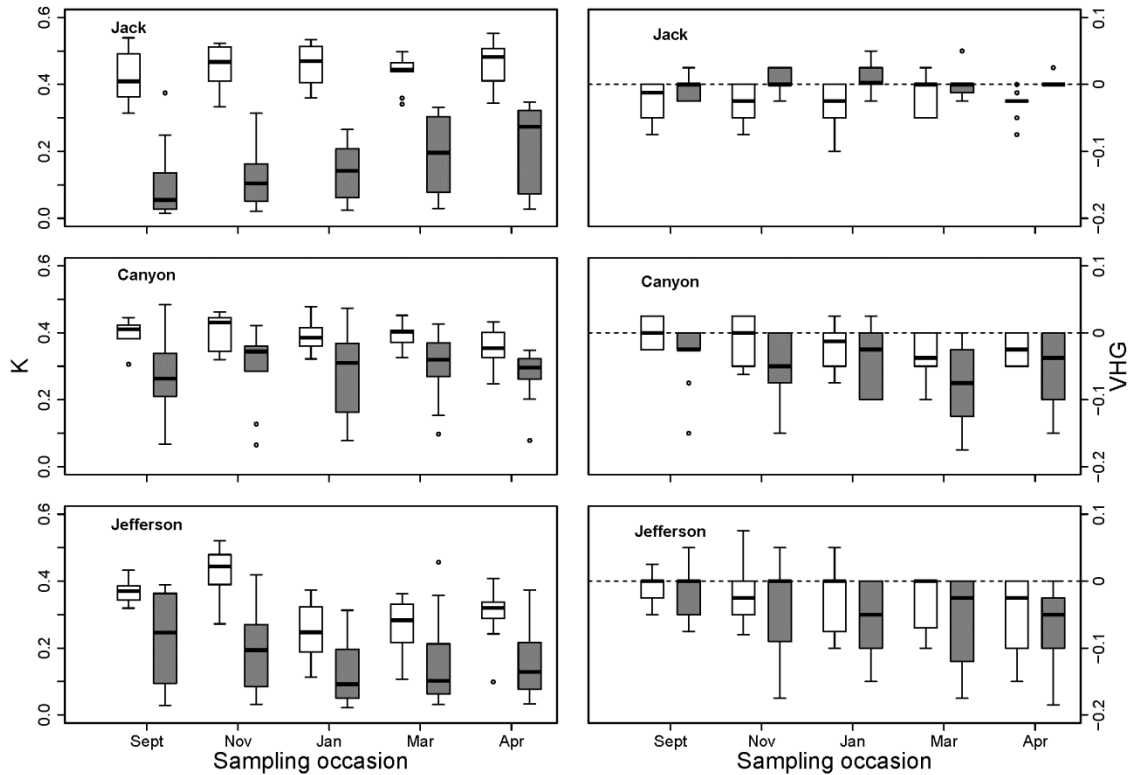


Figure 2.6. Sediment hydraulic conductivity (K ; $\text{cm} \cdot \text{s}^{-1}$; left panel) and vertical hydraulic gradient (VHG; right panel) in each of the three study areas measured in reds (open boxes) and in undisturbed sediment adjacent to reds (near-reds; dark gray boxes). VHG is negative when downwelling is present and positive when upwelling occurs. A dashed line is set at 0 for reference. Boxes represent the upper and lower quartiles, the mid-line represents the median value, whiskers depict the maximum and minimum values, excluding outliers (shown by dots).

CHAPTER 3

INCORPORATING MOVEMENT PATTERNS TO IMPROVE SURVIVAL ESTIMATES FOR JUVENILE BULL TROUT^{2,3}

Abstract

Populations of many fish species are sensitive to changes in vital rates during early life stages, but our understanding of factors affecting growth, survival, and movement patterns is often extremely limited for juvenile fishes. These critical information gaps are particularly evident for bull trout *Salvelinus confluentus*, a threatened Pacific Northwest char. We combined several active and passive mark-recapture and resight techniques to assess migration rates and to estimate survival for juvenile bull trout (70-170 mm total length). We evaluated the relative performance of multiple survival estimation techniques by comparing results from a common Cormack-Jolly-Seber (CJS) model, the less widely used Barker model, and a simple return rate (an index of survival). Juvenile bull trout of all sizes emigrated from their natal habitat throughout the year, and thereafter migrated up to 50 km downstream. With the CJS model, high emigration rates led to an extreme underestimate of apparent survival, a combined estimate of site fidelity and survival. In contrast, the Barker model, which allows survival and emigration to be modeled as separate parameters, produced estimates of survival that were much less biased compared with the return rate. Estimates of age-class-specific annual survival from the Barker model based on all available data were $\hat{S} = 0.218 \pm 0.028$ (estimate \pm SE) for age-1, and $\hat{S} = 0.231 \pm 0.065$ for age-2 bull trout.

² Chapter co-authored by Tracy Bowerman and Phaedra Budy

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This research demonstrates the importance of incorporating movement patterns into survival analyses, and we provide one of the first field-based estimates of juvenile bull trout annual survival in relatively pristine rearing conditions. These estimates can provide a baseline for comparison of future studies in more impacted systems, and will help managers develop reliable stage-structured population models to evaluate future recovery strategies.

Introduction

Knowledge of a species' life history and associated vital rates is crucial for development of effective conservation and recovery strategies (Williams et al. 2002). For many fish species, population dynamics are extremely sensitive to changes in survival at early life stages (Houde 1994; Hillborn et al. 2007). However, demographic rates are often difficult to assess between egg deposition and subadult stages, in part because survival rates during early stages are typically relatively low and can be highly variable (Bradford 1995). Although they are sometimes costly to obtain, life-stage-specific estimates of survival can be used to evaluate the relative contribution of various subadult stages to overall population change and identify targets for management (Caswell 2001; Morris and Doak 2003; Gross et al. 2006). Further, precise estimates of survival can help managers comprehend the magnitude of variability that may occur naturally as a result of environmental factors, such as density-dependent interactions, relative to anthropogenic influences (e.g., Johnston et al. 2007).

Mark-recapture studies provide a means to estimate survival and other key demographic information specific to individual cohorts or life stages (e.g., Lebreton et al. 1992; White and Burnham 1999). However, estimation of demographic rates may be

complicated for highly migratory species, both because of the effort needed to recapture mobile individuals and because animal movement patterns can affect interpretation of survival estimates (Cilimburg et al. 2002; Horton and Letcher 2008). For example, estimates of apparent survival (ϕ) generated using the common Cormack-Jolly-Seber (CJS) model are a combined estimate of true survival and site fidelity, the probability that an animal remains available for recapture within the study area (White and Burnham 1999; Sandercock 2006). With CJS estimates, it is not possible to distinguish permanent emigration from mortality, or temporary emigration from capture probability (Barker et al. 2004; Horton and Letcher 2008). As such, frequent emigration of marked organisms from the study area can confound estimates of apparent survival, and this issue has previously limited studies that sought to estimate survival of migratory stream-dwelling fishes (e.g., Paul et al. 2000; Letcher and Gries 2002). However, recent advances in technology have allowed researchers to improve recapture and resighting probabilities, while simultaneously, new analytical techniques have improved the ability to incorporate movement patterns into mark-recapture survival analyses.

The use of passive integrated transponder (PIT) tags has become increasingly common in fisheries research. Novel technology, including mobile PIT-tag readers and passive (stationary) in-stream antennas, now often accompany use of PIT tags. These technical advances offer a promising means of increasing the spatial and temporal extent of resight information (Zydlewski et al. 2006). Fish marked with PIT tags can be located by a researcher actively moving a mobile PIT-tag reader through a study site (e.g., Roussel et al. 2000). In comparison, a passive in-stream antenna (PIA) can be operated continually to detect PIT-tagged fish as they swim past a stationary location in the

stream. Both of these methods allow detection (i.e., resight) of marked individuals without handling or harassment.

Although PIT-tag data acquired at PIAs can help describe fish movement patterns within a stream system, resight data collected on a continual basis cannot be incorporated into many standard mark-recapture survival models. In the common CJS model, for example, captures and recaptures must take place over a short time period relative to the time between sampling events to ensure that survival probability is constant among individuals (Lebreton et al. 1992). A more recent model developed by Barker (1997) similarly requires captures during discrete events, but in addition, can also incorporate resights of marked animals during the intervals between discrete sampling periods. Whereas captures usually occur within a specific study area, resights of marked animals are assumed to take place throughout the range of the population of interest. Inclusion of this information allows for direct estimation of true survival and site fidelity as distinct parameters (Barker and White 2001; Barker et al. 2004). This model is uncommon in the fisheries literature (but see Buzby and Deegan 2004; Al-Chokhachy and Budy 2008), although it appears promising for studies that include numerous data types (Barker et al. 2004), or for fishes that exhibit coexisting life-history strategies and diverse migration patterns (Buzby and Deegan 2004; Horton and Letcher 2008).

One such fish species that demonstrates a range of movement patterns is the bull trout *Salvelinus confluentus*. The bull trout is a threatened species of stream-dwelling char that exhibits variability in life-history types, migration patterns, and maturation schedules (Bahr and Shrimpton 2004; Johnston and Post 2009). Bull trout populations often include both migratory and non-migratory (resident) life-history types (McPhail and

Baxter 1996; Homel et al. 2008). Adults typically spawn in cold, headwater streams which also serve as rearing habitat for juveniles. Bull trout usually disperse between ages 1 to 4, migrating downstream into larger river systems and lakes where they may reside for several years before returning to natal waters to spawn, although resident adult bull trout may inhabit upper portions of a watershed throughout their lives (Fraley and Shepard 1989; Ratliff 1992; Rieman and McIntyre 1993). For bull trout, high within-population variability and behavioral plasticity encumber the quantification of movement patterns and survival estimates. Bull trout migration distances can range from just a few kilometers to more than 200 km (McPhail and Baxter 1996; Hogen and Scarnecchia 2006), further complicating estimation of demographic parameters.

Considerable research has been conducted to describe migratory behavior and habitat use for individual bull trout populations (Swanberg 1997; Bahr and Shrimpton 2004; Watry and Scarnecchia 2008), but the majority of these studies have focused on adults. Information about bull trout life-history requirements and vital rates is still relatively sparse, particularly for early life stages. Very few studies have assessed juvenile bull trout migration patterns, rates of survival, or environmental factors affecting survival. Life-stage-based population projection models developed for bull trout suggest that population growth may be most sensitive to changes in survival of large adults and early life stages (Rieman and McIntyre 1993; Al-Chokhachy 2006). However, the predictive ability of such models is currently limited by a lack of empirical survival estimates specific to subadult stages.

To our knowledge, reliable estimates of survival for juvenile age classes (<120 mm total length; TL) are unavailable for bull trout. Previous studies assessed relative

survival for early age classes of bull trout by comparing abundances between years, but did not establish precise juvenile survival estimates (Paul et al. 2000; Johnston et al. 2007). Al-Chokhachy and Budy (2008) used mark-recapture methods to develop stage-specific survival estimates for bull trout larger than 120 mm TL, but did not include smaller individuals. Obtaining survival estimates specific to juvenile stage classes will help fill an important gap in our understanding of factors that determine bull trout survival at different life stages. Estimates of stage-specific survival rates will also aid in identifying life stages to target for recovery, and improve the ability of population models to predict population-level responses to environmental changes.

To evaluate migration patterns and estimate survival rates for juvenile bull trout, we conducted an intensive mark-recapture study within one of several important spawning areas used by a relatively large population of bull trout in the South Fork Walla Walla River (SFWWR), Oregon. The population of bull trout in the SFWWR exhibits both migratory and resident life-history forms (Homel et al. 2008), and migration distance and timing can be highly variable (Homel and Budy 2008). Prior to this study, little was known about juvenile bull trout dispersal and survival rates in this system.

The overall goal of this research was to provide insight into a stage of bull trout life history which has previously not been well quantified, and which has important implications for understanding how juvenile life stages affect population growth and persistence. To meet this goal, the specific objectives of this study were to: (1) quantify and better understand movement patterns exhibited by juvenile bull trout (70-170 mm TL), and (2) incorporate knowledge of juvenile migration rates into mark-recapture

analyses to obtain the most precise estimates of survival for bull trout during these influential early life stages.

Methods

Study Area

We conducted this study throughout approximately 600 m of Skiphorton Creek, directly upstream of the confluence with the South Fork Walla Walla River (SFWW), Oregon (Figure 3.1). Skiphorton Creek originates in the foothills of the Blue Mountains in northeastern Oregon and enters the SFWW approximately 113 km upstream from the Columbia River. The Skiphorton Creek study area has an average slope of 3 to 5%, mean width of 5 m, and mean water depth of 0.24 m. The study area is characterized by complex habitat, including numerous small side channels, pools, undercut banks, and large woody debris. Bull trout primarily use Skiphorton Creek for spawning and juvenile rearing, and the fish assemblage is composed of juvenile or small resident bull trout (primarily <170 mm TL) and rainbow and/or juvenile steelhead trout *Oncorhynchus mykiss*. Skiphorton Creek is located on roadless forest lands, and owing to the remote location, sampling was limited to the snow-free months of June through October.

We also gathered additional data throughout the SFWW and mainstem Walla Walla River (WW), both considerably larger streams than Skiphorton Creek. Bull trout spawn throughout approximately 20 km of the upper SFWW and tributaries, and adult and subadult bull trout use the entire SFWW and WW (43 and 81 km in length, respectively) for migration and overwintering habitat (Anglin et al. 2009).

Mark, Recapture, and Resight Techniques

Mark and recapture.— We conducted two discrete mark-recapture sampling events during the summers of 2007 and 2009, and three in 2008 (Table 3.1). We captured bull trout in Skiphorton Creek by chasing fish with a low-voltage electrical current downstream into a seine (hereafter referred to as “electroseining”). We constrained the number of electroseining events to minimize stress to juvenile fish, and we gathered initial data on all captured fish between 70 and 170 mm TL. We anaesthetized, weighed, measured, and marked bull trout with both an external fin clip and an internal PIT tag (12.5 mm FDXB), surgically inserted into the peritoneal cavity. We double-marked all individuals to identify recaptures and quantify tag retention rates. We checked all recaptured fish for tag loss, and recorded the unique PIT-tag code. We released all fish near the point of capture after full equilibrium had been restored.

Mobile resights.—In 2008 and 2009, we also used a mobile PIT-tag reader to detect marked fish throughout the Skiphorton Creek study area. We refer to this type of sampling as “mobile resight” surveys to remain consistent with literature on Barker models, in which the term “resight” has been used to refer to any method for obtaining observations of marked animals other than physical live recaptures. The mobile reader consisted of a backpack-mounted tuner and receiver connected to a 0.35 by 0.35 m triangular antenna at the end of an extendable pole (Biomark BP portable antenna; see Roussel et al. 2000; Cucherousset et al. 2005; Keeler et al. 2007). The reader’s maximum vertical PIT-tag detection distance ranged between 0.15 and 0.35 m, depending on the orientation of the tag and the reader’s tuning. Lateral read-range was extremely

limited, such that a PIT tag had to be directly below the triangular antenna to be identified.

During each mobile resight survey, the operator waded upstream through the entire study area, passing the reader over all areas of the streambed at a height that would allow for PIT-tag detection. The operator recorded the date, time, and exact location of each PIT tag. Each mobile resight sampling period took approximately 8 h, and all surveys were conducted by the same person to minimize sampling variability. We performed mobile resight surveys both during the day and at night and compared the recapture probability between these two time periods. We generally conducted mobile resight sampling approximately one week after electroseine mark-recapture events (Table 3.1) to assess mortalities following tagging.

Tag recoveries.—During the mobile resight surveys, we did not actually see marked fish, so we could not be certain whether (1) the PIT tag had been shed from a fish that was still alive, (2) the PIT tag was in a live fish, or (3) the marked fish had died but the tag remained in the river. We addressed the first possibility by double marking all fish with both a PIT tag and external fin clip. Because the observed rate of PIT-tag retention was high (see results), we assumed that immobile tags represented dead fish. We distinguished between a live resight and a “tag recovery” in the following manner: after detecting a PIT tag with the mobile reader, the operator tapped on the substrate adjacent to the tag location, and if the tag was in a different place following the disturbance, the observation was considered a live resight. To be considered a tag recovery, a PIT tag had to be found immobile in the same location during two consecutive mobile surveys. Although we did not actually observe dead fish, we used the

term “recovery” to describe detections of immobile PIT tags, to remain consistent with previous mark-recapture literature in which the term “dead recovery” has been used (Barker et al. 2004).

Passive in-stream antenna arrays and ancillary resight data.— In addition to sampling within the Skiphorton Creek study area, we also collected continuous resight data from marked fish as they swam past stationary PIAs. As part of a large-scale, multi-year research project (see Al-Chokhachy and Budy 2008), five PIAs operated in the SFWW and WW river system, located approximately 7, 16, 38, 52, and 103 km downstream from the Skiphorton Creek study area (Figure 3.1). The devices operated year-round, except for short time periods when maintenance was required, and enabled us to gather resight data at multiple locations outside of the immediate study area. In 2008 and 2009, we installed one additional PIA at the downstream end of Skiphorton Creek (Skiphorton PIA) to identify when fish emigrated from the study area. We used a solar panel to generate power for the remote site; the PIA only operated between 24 July and 28 September 2008, and from 8 June to 30 September 2009, when sufficient sunlight was available.

Bull trout marked in Skiphorton Creek were also recaptured throughout the entire SFWW and WW system via several different methods. Each summer, as part of the larger study mentioned previously, approximately 20 km of the SFWW were sampled for bull trout via electroseining, and all recaptures of fish marked in Skiphorton Creek were recorded. Marked bull trout were also recaptured throughout the year at screw traps and via research-related angling at multiple locations on the WW. Fish recaptured in the SFWW or WW were considered “ancillary resights,” collected during the intervals

between discrete mark-recapture sampling periods. Although ancillary resights made up a small proportion of the total data, this additional sampling allowed us to consider marked fish to be at risk of recapture anywhere in the geographic range of interest (Barker 1997; Barker et al. 2004).

Juvenile Movement Patterns

We evaluated the timing, direction, distance, and frequency of juvenile bull trout movement within the study area and throughout the SFWW and WW based on data combined from all of the sampling methods described above. We assumed that any marked fish that was detected in the SFWW or WW or resighted at the Skiphorton PIA had emigrated from the study area. We considered the assumption of emigration valid for the duration of our study because we observed no marked fish to have re-entered Skiphorton Creek after having left. For fish detected at the Skiphorton PIA, we used data from physical recaptures to estimate the length at emigration based on a linear equation for absolute growth rate applicable to short time scales (Isely and Grabowski 2007), where

$$Length_{emigration} = Length_{tag} + 5.23 + 0.099(time_{emigration} - time_{tag}).$$

We used movement observations to describe emigration rates and timing, and examined the impact of emigration on survival estimates.

Survival Analyses

We estimated annual survival probability for two separate age classes of juvenile bull trout: age-1 (70-120 mm TL) and age-2 (121-170 mm TL) where length-at-age at initial capture was estimated based on combined length-frequency analyses and otolith

aging (Al-Chokhachy and Budy 2008; Budy et al. 2011). All survival analyses were conducted in Program MARK (White and Burnham 1999). First, we estimated apparent survival from a CJS model (Cormack 1964; Jolly 1965; Seber 1965), a model commonly used to assess survival probabilities for a wide range of taxa (e.g., Lebreton et al. 1992; Muir et al. 2001; Letcher and Gries 2002). The CJS model only incorporates data obtained from discrete mark-recapture sampling periods, so we only used data collected during electroseine mark-recapture and mobile resight sampling in Skipthorton Creek. We combined mobile resights with active captures in the same discrete sampling period, as mobile resight surveys were conducted shortly after mark-recapture periods. The two parameters estimated by the CJS model are apparent survival (ϕ_i), the probability that an animal survives and remains in the sample from time i to $i + 1$, and p_i , the probability of encountering an individual given that it is alive and in the sample. Because emigration can confound these two parameters, we also used an ad hoc method in the CJS model to account for known emigration: when we observed an individual emigrate from the study area, we removed its contribution to survival parameter estimation at that time (see Horton and Letcher 2008). We included only known emigrants in this approach, which did not allow us to account for incomplete detection of emigrants.

We compared estimates of apparent survival from the standard and ad hoc CJS models with estimates of survival from the Barker model (Barker 1997; Barker and White 2001). As in the CJS model, mobile antenna resights from within the study area were incorporated into the data from the previous mark-recapture period. In addition to this data, the Barker model also allowed inclusion of data obtained during the interval ($i, i + 1$) between discrete sampling events, which included tag recoveries, resights at PIAs,

and ancillary resights throughout the SFWW and WW. If an individual was either recaptured or resighted on more than one occasion during the interval $(i, i + 1)$, only a single detection was recorded in the encounter history (Barker et al. 2004). The model complexity necessary to accommodate this additional data results in a total of seven parameters in the Barker model (Barker 1997). In addition to survival (S_i) and capture (p_i) probabilities, other parameters include F_i , the probability that an animal at risk of capture at time i is at risk of capture at time $i + 1$ (i.e., has not emigrated from the study area), F'_i , the probability that an animal not at risk of capture at time i is at risk of capture at time $i + 1$ (e.g., temporary emigration), R_i , the probability that an animal alive at time i is resighted alive in $(i, i + 1)$, and R'_i , the probability that an animal is resighted before it dies in $(i, i + 1)$. A final parameter, r_i , the probability that an animal dies and is found dead in the interval $(i, i + 1)$, allowed us to incorporate data from tag recoveries. Because we recovered only a relatively small number of tags, we also compared survival estimates between a data set that included tag recoveries, and another which did not, where we set $r = 0$.

We assessed model fit using the median \hat{c} approach in program MARK to estimate a variance inflation factor (\hat{c}) for the most saturated model given available data (e.g., Horton et al. 2011). Because the variance inflation factor was reasonable ($\hat{c} = 1.98$) and we expected that model fit improved with the inclusion of individual covariates, we based model selection on Akaike's Information Criterion corrected for effective sample size (AICc). We considered models with a difference of 0-2 AICc to have substantial support, models with >4 to have considerably less support, and models with >10 to have virtually no support (Burnham and Anderson 2002). Data limitations and model

parsimony led us to model some parameters as constant across time and between size classes.

Our primary parameter of interest was survival, so we used a two-step approach to the model selection process. Initially, we retained high dimensionality in our survival parameters (ϕ in the CJS model and S in the Barker model), and iteratively modeled the remaining parameters based on a priori knowledge of sampling efficiency and bull trout ecology. With the CJS model, model selection of the less pertinent parameter, recapture probability (p), resulted in a set of candidate models for which p varied as a function of increasing trend across sampling periods and with length as an individual covariate. For all candidate Barker models, we modeled p as a function of individual length and r as constant over time and among size classes. Owing to the variability in resights among sampling intervals (Table 3.1), we modeled both R and R' as a function of time. Finally, we found strong support for models in which we explicitly modeled permanent emigration by setting $F' = 0$ and where F varied as a function of individual length.

After selecting the model structure for the less pertinent parameters, we then focused on modeling survival, the parameter of greatest interest (e.g., Slattery and Alisauskas 2002; Collins and Doherty 2006). In both CJS and Barker candidate model sets, we estimated survival for the two different age classes as separate groups, and modeled survival in relation to factors determined a priori, including annual variation, time interval, season, and individual covariates measured at the time of tagging, such as length. In addition, we included models with a marking effect to test the hypothesis that survival rates might be lower during the time interval immediately following initial capture. To facilitate comparison of survival estimates and variance between the CJS and

Barker model types, we present estimates from the single best model from the set of candidate models.

We compared survival estimates from the top CJS and Barker models with an estimate of the return rate, an index of survival. Return rates can be considered a minimum estimate of true survival, because they do not account for detection probability or site fidelity (Sandercock 2006). We estimated a simple return rate by calculating the proportion of marked fish in each size class that were recaptured or resighted nine or more months after initial tagging (fish that survived until the subsequent field season and afterward). We estimated a return rate (\widehat{RR}) for marked fish from a simple proportion with binomial variance using:

$$\widehat{RR} = \frac{Y}{N}$$

$$var(\widehat{RR}) = \frac{RR(1-RR)}{N}$$

where Y represents the number of marked fish that were resighted, and N is the total number of marked fish.

Results

Recaptures and Resights of Marked Fish

Between 2007 and 2009, we marked 669 bull trout in Skiphorton Creek. Nearly 50% were recaptured or resighted at least once ($n = 327$), and approximately 11% multiple times ($n = 71$). The total number of unmarked fish caught in a single mark-recapture sampling period ranged between 52 in May 2008 and 142 in July 2009 (Table 3.1). The majority of bull trout captured and PIT tagged were in the age-1 class, whereas only 25% of marked individuals were > 120 mm TL (Figure 3.2).

Multiple techniques were necessary to obtain sufficient data to track movement patterns of marked individuals and evaluate survival rates, although the efficiency of resighting techniques varied. Data from the mobile PIT-tag reader, all PIAs combined, and ancillary resights accounted for 62%, 36%, and 2% of total resight observations, respectively. The number of fish resighted during each interval between discrete sampling periods increased over the duration of the study (Table 3.1), as both the number of marked fish and sampling effort increased. In 2007, we resighted no fish between the two summer capture periods, and only six between the 2007 and 2008 field seasons. After we added the PIA at the lower end of the Skiphorton Creek study area during 2008 and 2009, PIA resights increased dramatically.

The mobile PIT-tag reader enabled us to resight marked bull trout while minimizing disturbance to the stream and fish, and was particularly effective when used at night (Table 3.2). The probability of detecting a PIT-tagged fish was 4.5 times greater during mobile resight sampling conducted at night ($p = 0.51 \pm 0.04$; estimate \pm SE) compared with daytime sampling ($p = 0.11 \pm 0.02$), and 2.5 times greater than the probability of recapturing a marked fish using electroseining ($p = 0.22 \pm 0.03$). We recaptured only one fish that had shed its PIT tag, resulting in an estimate of 98.8% tag retention. Given this high rate of tag retention, we did not explicitly account for tag loss, and considered the 12 tag recoveries found during 2008 and 2009 to represent mortalities in our analyses.

Juvenile Bull Trout Movement Patterns

Recapture data collected via multiple methods allowed us to determine when juvenile bull trout emigrated from the natal spawning/rearing tributary, and enabled us to

observe bull trout movements throughout the study area and larger SFWW and WW system. Within the Skiphorton Creek study area, juvenile bull trout moved both upstream and down, but the predominant direction of movement was downstream (Figure 3.3). Movement in the upstream direction occurred at low frequencies within the study and the largest recorded upstream movement was only 0.2 km. We observed numerous juvenile bull trout that remained for more than one month within 50 m of their original capture location, and in many instances, those fish were located in the same habitat unit (e.g., a small pool or eddy) during numerous consecutive sampling periods. The majority of marked fish remained within 0.5 km of their initial capture location until they began a downstream migration, after which many moved rapidly downstream, some traveling up to 6 km in 3 days. We resighted marked fish at various locations throughout the larger SFWW and WW, and the greatest observed travel distance was 53 km downstream from the study area. We did not detect a relationship between stream discharge and movement patterns (Figure 3.3).

Juvenile bull trout emigrated from the study area at a range of sizes and during all seasons. Based on a linear relationship between juvenile bull trout growth rate over time, we estimated the length of marked fish for which the exact date of emigration was known (i.e., fish detected passing the Skiphorton PIA). Juvenile bull trout of all sizes exceeding 80 mm TL emigrated from the study area, although the majority of emigrants were longer than 100 mm (Figure 3.2). The proportion of emigrants increased with fish length, but we did not observe a distinct size threshold at which movement was initiated. Emigration occurred throughout the year, with a slight increase in the emigration rate during late August through October. In the age-1 class, 52% of fish recaptured between 4 and 12

months after initial capture had moved more than 4 km downstream of the study area, and 92% of the age-2 fish appeared to have emigrated (Figure 3.4). As a result of high emigration rates and variable emigration timing, a substantial proportion of marked fish were unavailable for recapture during subsequent sampling periods. Furthermore, no marked fish were detected within the study area more than 18 months after tagging, suggesting that nearly all juveniles emigrated from their natal habitat between age 1 and age 3.

Juvenile Bull Trout Survival Rates

Estimates of survival based on the simple return rate were $\widehat{RR} = 0.171 \pm 0.017$ (estimate \pm SE) for the age-1 class, and $\widehat{RR} = 0.190 \pm 0.030$ for the age-2 class (Figure 3.5). Compared with the return rate, estimates of apparent survival from the naïve CJS model were biased extremely low but improved when emigration was included in the models via the ad hoc approach. Point estimates of annual survival using the Barker model were higher than the return rate, and the 95% confidence intervals encompassed the return rate. Across models, the variance associated with survival estimates was greater for age-2 fish, as there were fewer fish marked in this size class.

The CJS model that minimized AICc was constant across time, and included separate estimates of apparent survival for the two age classes and fish length as an individual covariate (Table 3.3). From this model, the estimate of annual apparent survival for the age-1 class was $\phi = 0.090 \pm 0.018$ for a fish with mean length 100 mm TL, and $\phi = 0.009 \pm 0.009$ for the age-2 class based on a mean length of 133 mm. Compared with the return rate, CJS estimates accounted for only 52% and 5% of the return rate for the two size classes, respectively (Figure 3.5). The ad hoc CJS approach

resulted in the same best model as the naïve CJS model, and with emigration explicitly incorporated, survival estimates were $\phi = 0.142 \pm 0.023$ for the age-1 class, similar to the return rate, but $\phi = 0.069 \pm 0.030$ for the age-2 class, which was only 36% of the return rate. Model selection showed much less support for the model that included a tagging effect compared with the top ranking model, and a likelihood ratio test also provided no evidence of a difference in survival during the time period immediately following tagging, ($\chi^2 = 1.112$, $df = 2$, $P = 0.57$).

In contrast to the CJS model results, annual survival estimates from the Barker model were somewhat higher than estimates from the return rate (Figure 3.5). Model selection produced identical model ranking for data with and without tag recoveries, but led to slightly different estimates of survival with similar precision. For both data sets, the model with the greatest support was one in which survival was constant across time and varied between size classes (Table 3.3). Estimated annual survival for the Barker model including dead recoveries was $\hat{S} = 0.218 \pm 0.028$ for fish the age-1 class, and $\hat{S} = 0.232 \pm 0.065$ for age-2 fish. When tag recoveries were omitted from the data ($r = 0$), the same best-ranking model provided similar estimates of $\hat{S} = 0.195 \pm 0.026$ and $\hat{S} = 0.191 \pm 0.062$, respectively. Based on AICc weights, there was little support for the model that included annual variability in survival, although this was unsurprising given only three years of data. There was also considerably less support for a model that included a tagging effect, and a likelihood ratio test provided no evidence of lower survival during the time period directly following tagging ($\chi^2 = 1.768$, $df = 2$, $P = 0.41$).

In addition to providing robust estimates of survival, the Barker model also included specific parameters to estimate site fidelity, providing additional insight into

juvenile bull trout migration patterns. Model selection demonstrated strong support for a model in which we explicitly modeled permanent emigration ($F' = 0$) compared with a model that included random emigration (Barker and White 2001), consistent with our movement observations. In this model, F varied as a function of individual length, and parameter estimates indicated that F was negatively related to fish length at marking and decreased sharply for fish larger than 100 mm. Estimates of F were 0.735 ± 0.151 for a fish measuring 90 mm TL, compared with 0.125 ± 0.063 for a 110 mm TL bull trout. This sharp decline in the probability of an individual remaining at risk of capture was consistent with our observations of emigration rates for bull trout across this range of sizes.

Discussion

Our results provide some of the first estimates of annual survival rates for age-1 and age-2 bull trout based on individual mark-recapture information. Use of multiple recapture and resighting techniques allowed us to assess rates of emigration from natal habitat and to describe movement patterns of juvenile bull trout. In addition, incorporating emigration into our survival analyses improved the accuracy of annual survival estimates for juvenile bull trout. Results from the Barker model appeared to be the least-biased estimates of survival based on the model types we considered, and are the most precise field-based survival rates available for juvenile bull trout of which we are aware. Our study demonstrates the importance of incorporating movement patterns into survival analyses for migratory species, and provides an important comparison of contemporary capture-recapture techniques in stream systems.

Mark, Recapture, and Resight Techniques

Use of PIT tags was highly effective in this study, as it enabled us to detect marked fish across a large geographic range with minimal handling. We recovered 2 of the 12 total tags during the sampling period directly after tagging, but based on our analyses, we found no evidence that PIT tagging individuals affected survival estimates. These results correspond with previous studies of juvenile salmonids, which have likewise detected no discernible difference in survival between PIT-tagged and non-tagged fish held in a controlled setting (Prentice et al. 1990; Gries and Letcher 2002) or in the wild (Ombredane et al. 1998).

Use of the mobile PIT-tag reader allowed us to increase the probability of resighting a marked individual while causing little disturbance to the stream and fish. The mobile reader was also an efficient use of sampling time, as it required only one person to operate (compared to three for the electroseine method) and the entire study area could be scanned in 8 h. The mobile reader was most effective when operated at night, when juvenile bull trout often moved very little from their location as the reader passed over them, even after the operator tapped on the substrate (in contrast with daytime sampling, when fish usually moved immediately). As a result, five resights were initially misidentified as tag recoveries, but the marked fish subsequently changed locations or were detected at downstream PIAs. Thus, we only classified tags as recoveries when they were found in the same place during at least two consecutive sampling periods.

We recovered only 12 tags, and this relatively small number may not have been sufficient to improve the precision of survival estimates from the Barker model.

Nonetheless, it is reasonable to expect that larger numbers of tag recoveries would yield greater precision in parameters of interest (Barker and Kavalieris 2001). Tag recoveries could also have represented PIT tags that were shed from fish that were still alive, rather than a true mortality. However, based on the high rate of PIT-tag retention we observed, we considered the probability of a shed tag unlikely and therefore did not incorporate tag loss rates in our survival estimates. Other studies of similar-sized juvenile fish have also shown high rates of PIT-tag retention (Ombredane et al. 1998; Gries and Letcher 2002). If PIT-tag retention was lower than we observed, we would have underestimated true survival (Knudsen et al. 2009), and our annual survival estimates would be conservative.

Passive in-stream antenna arrays at six locations stationed at various points throughout the geographic range of the population allowed us to collect data continually throughout the year, including in winter when our remote field site was inaccessible. Use of multiple PIAs also helped us develop a detailed spatial and temporal understanding of juvenile bull trout movement patterns and emigration rates. Detection efficiency varied among PIAs and at different discharges, but we did not have sufficient data or the analytical ability to incorporate this variability into our analyses. Operation of the PIA at the downstream end of the study area over the entire year would certainly have increased our knowledge of emigration timing and improved survival estimates from the ad hoc CJS method. However, the Barker model can incorporate data collected opportunistically (Barker 1997) and as such, allowed for inclusion of PIA data even when sites operated at less than 100% detection efficiency.

We observed an increasing trend in the number of recaptures/resights over the course of the study, which likely occurred as a result of increased effort and efficiency

over time. This increase in efficiency resulted from installation of the Skiphorton PIA, use of the mobile PIT-tag reader at night, and a potential improvement in the skill of the person operating the mobile reader. Due to high emigration rates, variation in emigration timing, and low capture probabilities of juvenile bull trout, multiple resight techniques were necessary to obtain sufficient resight data to estimate survival and to characterize movement patterns. Each of these techniques provided data that informed estimates of survival and emigration in a different way. While use of the mobile PIT-tag reader at night resulted in a relatively high capture probability compared with other methods, it only allowed detection of fish that remained in the study area. Data collected at PIAs were integral in monitoring movements throughout the broader range of the population, but the spatial and temporal scope of this research was possible only because a preexisting infrastructure of PIAs existed within the river system. The high cost of obtaining this type of information, both in terms of money and effort, may be prohibitive in many studies. In our research, it would not have been possible to reliably estimate survival without the use of additional resight methods both within and outside of the Skiphorton Creek study area. Thus, the cost of using various sampling techniques relative to information gained should be weighed carefully within the context of overall study objectives (e.g., Al-Chokhachy et al. 2009).

Juvenile Bull Trout Movement Patterns

Migratory behavior is known to vary among different age classes of bull trout and among populations (McPhail and Baxter 1996; Monnot et al. 2008). For the population of juvenile bull trout in Skiphorton Creek, emigration from the natal stream occurred across a range of sizes >80 mm TL, and rates of emigration increased with fish length.

These results are consistent with research in other locations where juvenile bull trout typically migrate from rearing areas into larger rivers between age 1 and 3, with the majority migrating at age 2 (Oliver 1979; McPhail and Baxter 1996). However, our research demonstrated that a surprisingly large proportion of age-1 juveniles (< 120 mm TL) emigrated from rearing habitat into the larger SFWW. These data suggest that as juveniles grow larger, selective forces favor migration downstream into larger, warmer, and more productive habitat, despite potentially greater risk of mortality from predators (e.g., adult bull trout) and environmental catastrophes, such as flooding. Our data also showed that after leaving their natal stream, juvenile bull trout migrated throughout more than 50 km of downstream habitat in the SFWW and WW, indicating that immature fluvial bull trout used a wide range of rearing habitat throughout the entire river network.

Over the course of this study, juvenile bull trout emigrated from spawning and rearing habitat continuously throughout the year. We observed a pulse of emigration into the SFWW and WW in July through October, when stream discharge is at its lowest, and instream barriers may be more difficult to pass. Increased observations during this time period may have been influenced by higher sampling intensity during these months, although other research has similarly demonstrated higher rates of downstream subadult migration during late summer and fall (Oliver 1979; Homel and Budy 2008). Immature bull trout also migrated downstream throughout the remainder of the year, including during winter months, a time period during which adult bull trout are often considered sedentary (Bahr and Shrimpton 2004; Watry and Scarnecchia 2008). These data illustrate the variability of juvenile bull trout migratory behavior, a component of the fluvial life history which is not always considered in management objectives.

Mark-Recapture Models and Annual Survival Estimates

Migration rates and distances are often difficult to quantify for species that exhibit diverse life-history characteristics, or variation in both migratory behavior and home range size, such as bull trout, coastal cutthroat trout *O. clarki clarki*, rainbow trout, and brook trout *Salvelinus fontinalis* (e.g., Trotter 1989; Rodriguez 2002; Meka et al. 2003). Nonetheless, understanding and incorporating movement patterns into capture-recapture studies can dramatically improve estimates of survival and other important vital rates (Cilimburg et al. 2002; Horton and Letcher 2008). In our study, continuous emigration from the study area resulted in a constant loss of marked fish from the study population. The return rate (the minimum estimate of true survival) was higher than the estimates of apparent survival using the CJS model because it included data from individuals resighted anywhere in the geographic range of the population, including fish that had emigrated from Skiphorton Creek. In contrast, the naïve CJS model only used data collected within the study area, from which marked fish emigrated continually, resulting in estimates of apparent survival that were considerably lower than the return rate. This bias was more pronounced for the age-2 class because fish in this size range demonstrated higher emigration rates. When we incorporated emigration directly into encounter histories, we observed an improvement over the naïve CJS model, but the ad hoc approach still produced estimates of apparent survival that were biased low, particularly for the age-2 size class.

In contrast to the CJS model, the Barker model produced estimates of annual survival which were higher than the observed return rate, and which were similar between the two size classes, or slightly greater for the age-2 size class compared with

the age-1 class. This latter observation indicates that bull trout survival rates may increase with size and age, which is consistent with many other fish species (Lorenzen 2006). Although we have no way of knowing true survival rates in the wild, it is reasonable to expect that true survival rates would be higher than the return rate, which does not account for recapture probability (Martin et al. 1995; Sandercock 2006). In simulation analyses, Horton and Letcher (2008) found that the Barker model yielded robust estimates of survival with very little bias, regardless of whether emigration was temporary or permanent. Given the robust nature of the Barker model and the relative agreement between annual survival estimates derived from this model and observed return rates, we believe that the best estimates for juvenile bull trout annual survival from our study are those obtained from the Barker model.

Our study provides an important baseline of field-based annual survival estimates for age-1 bull trout (70-120 mm TL). Prior to our study, survival of this age class represented a significant gap in our understanding of bull trout demography. Our estimates of annual survival rates are within the range of other annual survival estimates for juvenile brook trout, a closely related species (mean \pm SE apparent survival (ϕ) = 0.218 ± 0.149 ; Petty et al. 2005). For age-2 bull trout, survival estimates for fish marked in Skiphorton Creek were higher than from the larger SFWW River (Al-Chokhachy and Budy 2008), where estimates of annual survival for subadult bull trout 120-170 mm TL varied between 0.025 ± 0.009 and 0.154 ± 0.052 , depending on the year. Higher estimates of annual age-2 bull trout survival in this study compared with other research may reflect the greater sampling intensity in our study design, and it could also represent true biological differences in survival between stream types. Our results indicate that

survival rates for juvenile bull trout are higher in small tributaries compared with larger rivers, but also that fish emigrate from these tributaries as they mature. Together, these observations suggest that there may be a trade-off between the increased risks in large rivers (e.g., predation, catastrophic flooding), and faster growth rates associated with warmer, more productive waters (Selong et al. 2001). While emigration from small, hydrologically stable headwater streams may decrease the probability of survival, fish that do survive will likely grow faster than their counterparts that emigrate later. The variability in size at which juvenile bull trout emigrate from natal streams may represent an important adaptation that allows populations to hedge their bets in an unpredictable environment.

Conservation and Management Implications

This research describes movement patterns and survival rates for juvenile bull trout (<170 mm TL), and provides insight into a life stage that is not well understood. Our data demonstrate that juvenile (ages 1 and 2) fluvial bull trout exhibit a range of migratory behavior. In the SFWW, juveniles moved from natal rearing habitat to larger rivers throughout the year and across a range of sizes. Based on these data, maintaining diversity in life-history adaptations, including the variability in juvenile migratory behavior, may be important for long-term population persistence. Further, juvenile bull trout from 80-100 mm TL and larger used habitat throughout the SFWW and mainstem WW in all seasons, and these size classes should be considered in management decisions regarding flow regulation and fish passage. In addition to documenting juvenile migratory behavior, our research demonstrates the importance of incorporating

emigration rates into survival analyses for species that exhibit variable migration patterns, and improves our understanding of the influence of migration on survival rates.

We provide some of the first field-based, empirical estimates of juvenile bull trout annual survival based on marked individuals. These estimates can provide a baseline against which to compare future studies of juvenile bull trout survival in more impacted systems, as well as improve our understanding of how various management actions may affect bull trout at specific life stages. Given the sensitivity of bull trout population growth to variations in survival at early life-stages, stage-specific estimates of vital rates are important for the development and use of reliable stage-structured population models. Survival estimates from this research will help improve the predictive ability of bull trout population viability analyses, which can be used to evaluate population-level responses to different management scenarios, and to develop sound recovery plans for this imperiled species.

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Table 3.1. Sampling schedule and methods used to capture, recapture, or resight juvenile bull trout. Fish were captured by electroseining (ES) and resighted with a mobile PIT-tag reader (MPR) in Skipthorton Creek, Oregon. Marked fish were resighted during intervals between discrete sampling events at a passive in-stream antenna the downstream end of the study area (PIA_{SH}), and at five passive in-stream antennas (PIA_{WW}) as well as via ancillary captures (ANC) throughout the South Fork Walla Walla and Walla Walla rivers.

Sampling date	Resight interval (days)	Number marked	Live recaptures/resights	Live resights	Dead recoveries	Sampling method
Jul 10-13, 2007	--	86	0	--	--	ES
Interval	34	--	--	0	0	PIA _{WW} + ANC
Aug 14-15, 2007	--	65	14	--	--	ES
Interval	261	--	--	6	0	PIA _{WW} + ANC
May 2-3, 2008	--	52	5	--	--	ES
Interval	67	--	--	2	0	PIA _{WW} + ANC
Jul 7-8, 2008	--	94	3	--	--	ES
Interval	34	--	--	4	3	PIA _{WW} + ANC + PIA _{SH}
Aug 13-19, 2008	--	123	23	--	--	ES + MPR
Interval	293	--	--	62	5	PIA _{WW} + ANC + PIA _{SH}
Jun 8-15, 2009	--	107	12	--	--	ES + MPR
Interval	36	--	--	34	0	PIA _{WW} + ANC + PIA _{SH}
Jul 21-31, 2009	--	142	79	--	--	ES + MPR
Interval	363	--	--	101	4	PIA _{WW} + ANC + PIA _{SH}
Total	1108	669	136	209	12	

Table 3.2. Comparison of capture probability for capture and recapture/resight methods used to estimate juvenile bull trout movement and survival. The parameter p is the probability of capturing an individual given that it is alive and in the sample, R is the probability that an animal is resighted alive in the time interval $(i, i+1)$, and R' is the probability that an animal is resighted before it dies in $(i, i+1)$.

Sampling method	Data type	Capture probability (p or R)	SD	average recapture/ sampling hour
Eseine	live recapture	$p = 0.22$	0.03	0.76
Mobile antenna day	live resight in study area/dead recovery	$p = 0.11$	0.02	2.29
Mobile antenna night	live resight in study area/dead recovery	$p = 0.51$	0.04	7.55
PIAs + ancillary	live resight outside study area	$R = 0.19^*$	0.06	na
PIAs + ancillary	live resight outside study area	$R' = 0.16^*$	0.01	na

*Estimates of R and R' are for the time period when the Skipthorton PIA was operating continuously (maximum observed R).

Table 3.3. Survival models for juvenile bull trout captured and marked in Skipthorton Creek, Oregon, 2007-2009. Two age classes were modeled as separate groups: age-1 (70-120 mm total length; TL) and age-2 (121-170 mm TL). Period symbol indicates no difference across time or among groups, + denotes an additive parameter, = 0 indicates a parameter set to 0; length at capture was included as an individual covariate. Akaike's information criterion corrected for small sample (AIC_c), model likelihood, and number of parameters are shown.

Survival varies by	Candidate models	AIC_c	Model Likelihood	Num. Params.
CJS Models				
Age group + length	$\phi_{(group+length)} p_{(timetrend+length)}$	664.95	1.00	7
Age group	$\phi_{(group)} p_{(timetrend+length)}$	668.87	0.14	5
Year	$\phi_{(year)} p_{(timetrend+length)}$	681.87	0.04	6
Group + tag effect	$\phi_{(group+tag\ effect)} p_{(timetrend+length)}$	673.25	0.00	9
Barker models				
Age cohort	$S_{(group)} p_{(length)} r_{(.)} R_{(time)} R'_{(time)}$	1839.63	1.00	18
	$F_{(length)} F'_{(=0)}$			
age cohort + length	$S_{(group+length)} p_{(length)} r_{(.)} R_{(time)} R'_{(time)}$	1841.49	0.39	19
	$F_{(length)} F'_{(=0)}$			
Age cohort + tag effect	$S_{(group+tag\ effect)} p_{(length)} r_{(.)} R_{(time)}$	1844.35	0.09	20
	$R'_{(time)} F_{(length)} F'_{(=0)}$			
Year	$S_{(year)} p_{(length)} r_{(.)} R_{(time)} R'_{(time)} F_{(length)}$	1860.91	0.00	19
	$F'_{(=0)}$			

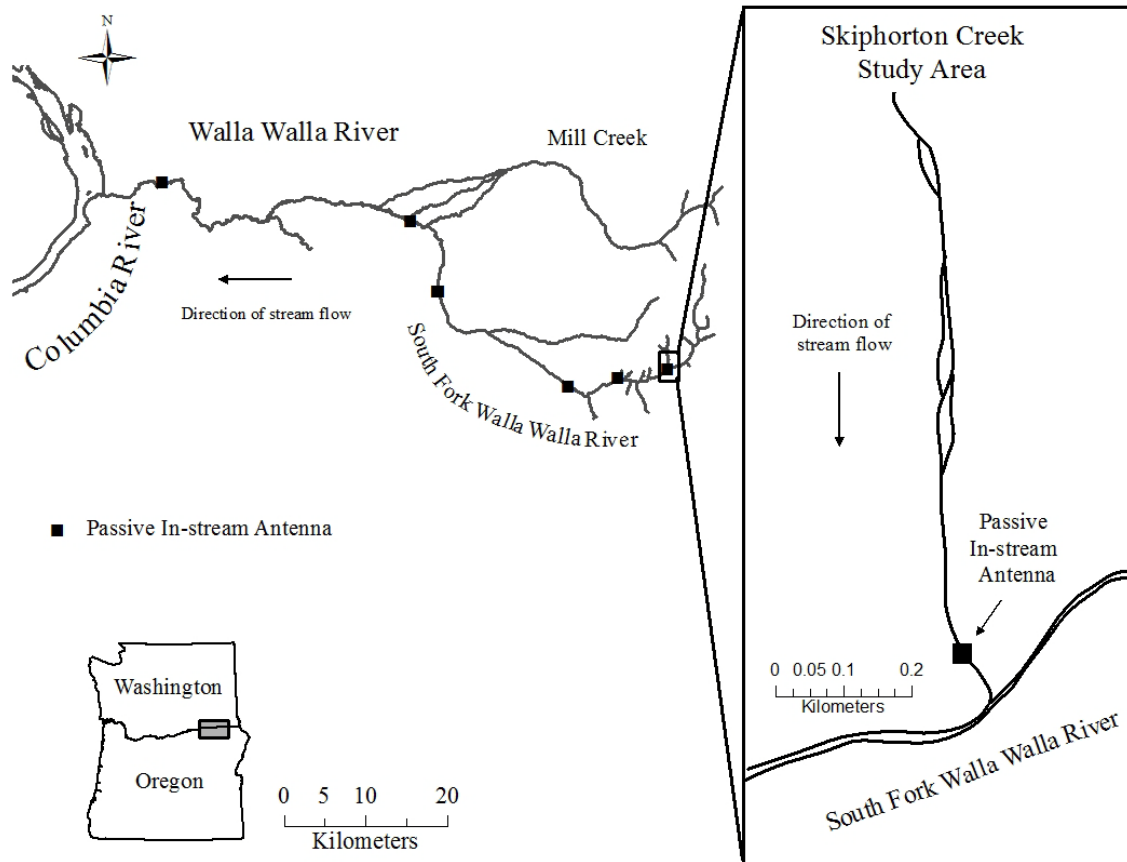


Figure 3.1. Map of the study area, Skiphorton Creek, Oregon, where juvenile bull trout were initially captured and marked. Marked fish could be resighted throughout the South Fork Walla Walla and Walla Walla rivers, including at any of the six passive in-stream antennas (PIAs) located downstream of the study area.

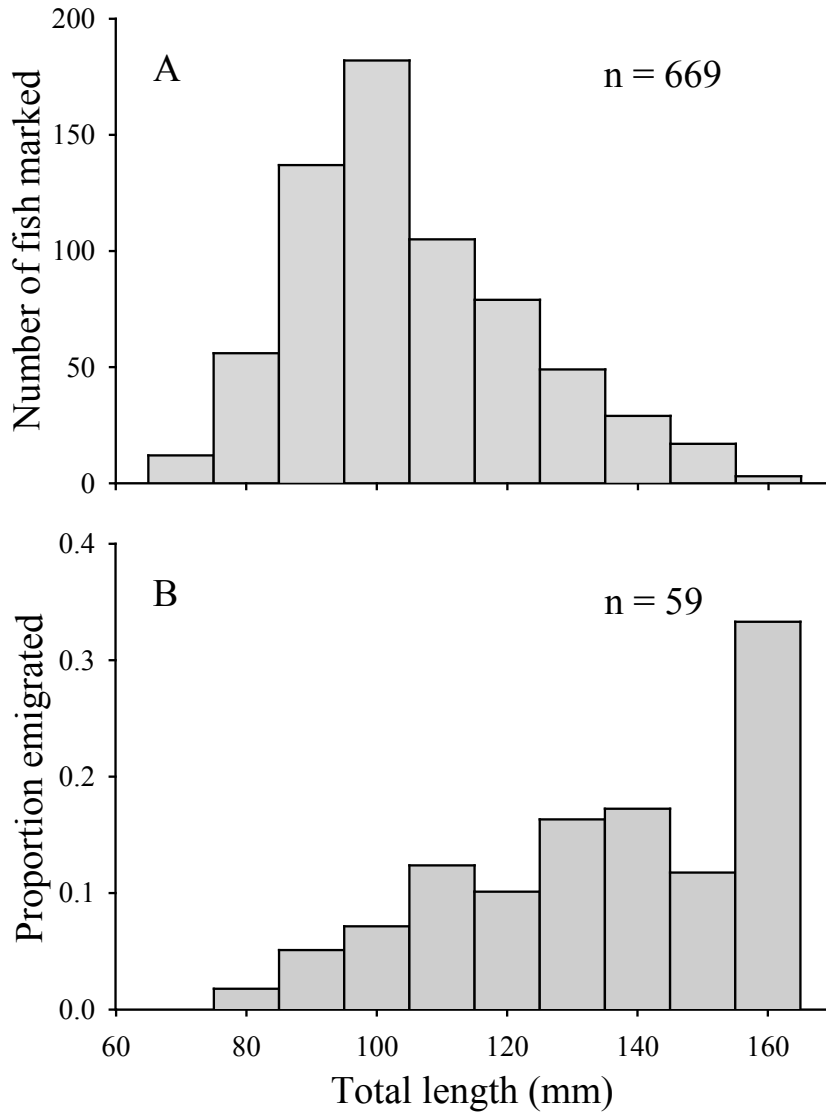


Figure 3.2. (A) Length at capture of juvenile bull trout caught in Skipthorton Creek, Oregon and marked with PIT tags. (B) The proportion of marked fish in each size group for which the exact date of emigration from the Skipthorton Creek study area was known. Emigration was determined when PIT-tagged fish were detected at a passive in-stream antenna located at the lower boundary of the study area. Length at emigration was estimated based on a linear growth relationship developed for the study population.

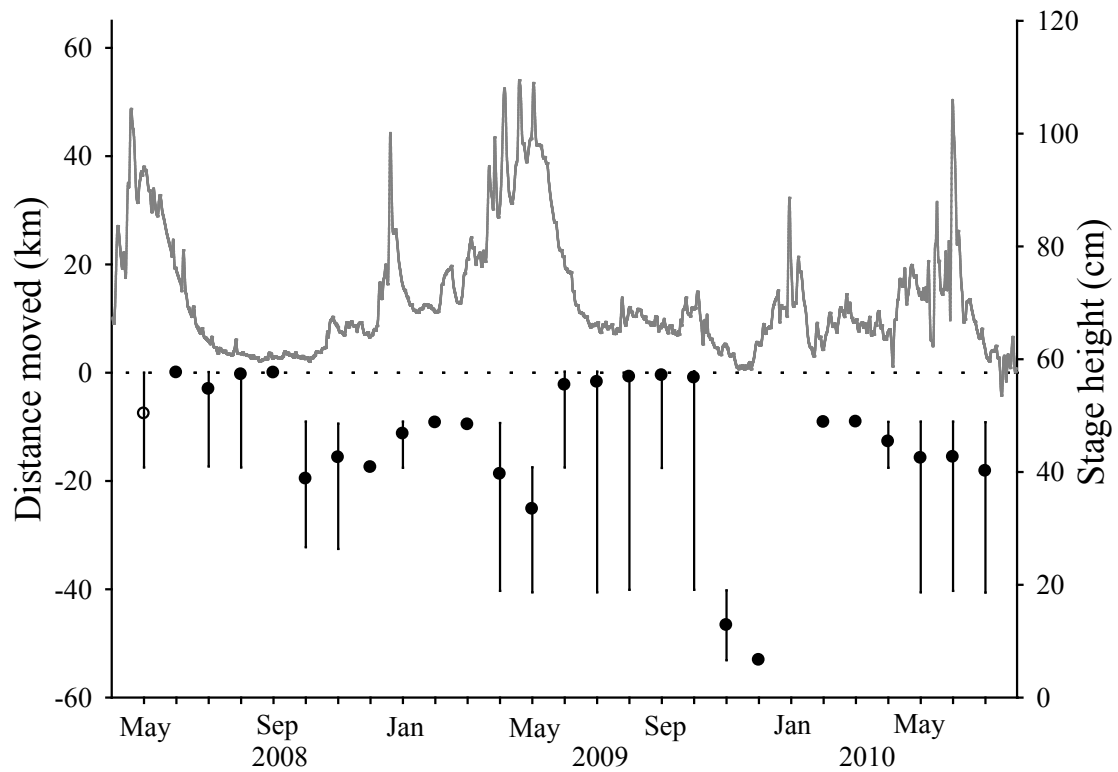


Figure 3.3. Direction of monthly juvenile bull trout migrations. Closed circles represent mean distance moved and bars represent the maximum and minimum distance traveled during the specified month. Positive distance values represent distance (km) moved upstream, and negative values represent distance moved downstream; a horizontal line at 0 is provided for reference. Stage height readings from the South Fork Walla Walla River are shown on the second y-axis.

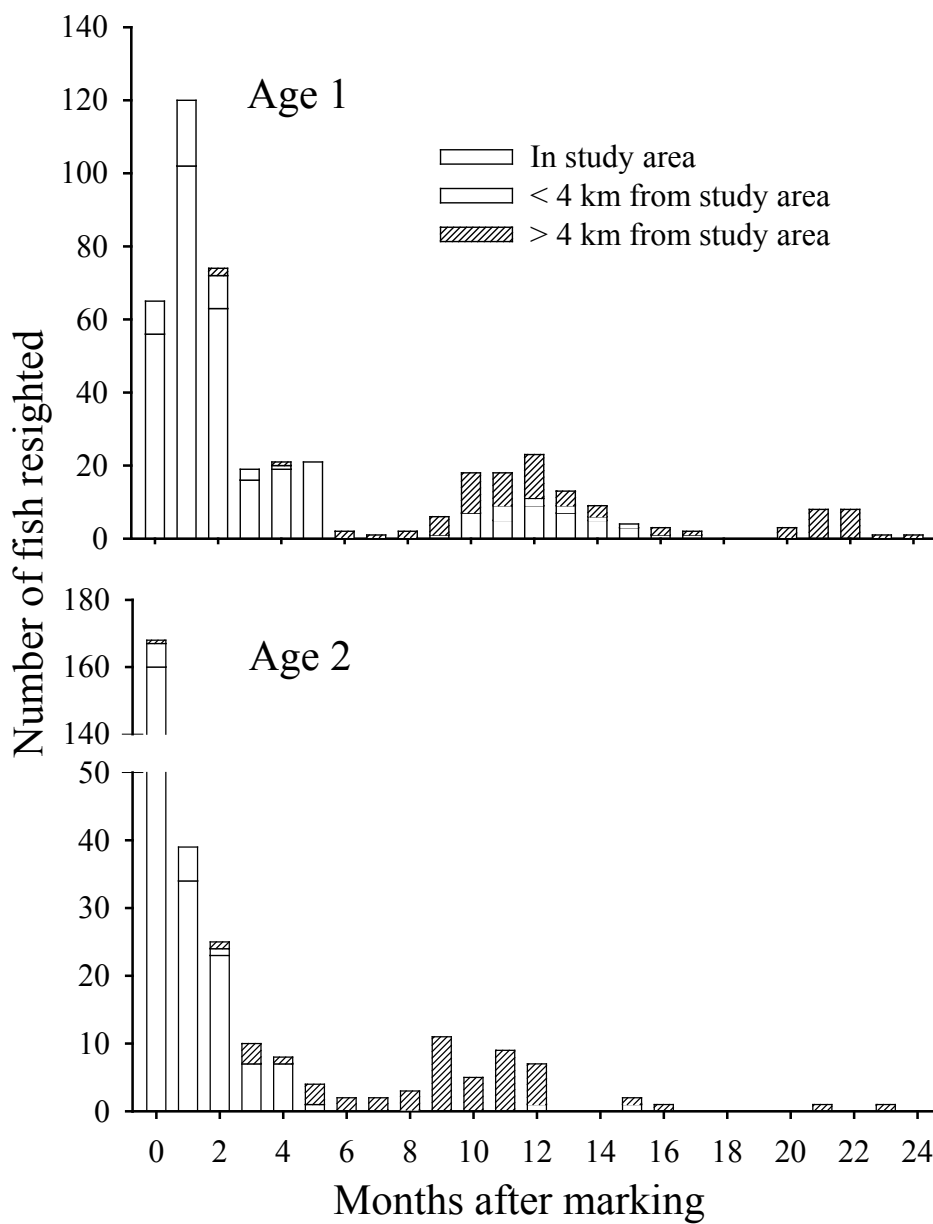


Figure 3.4. Number of juvenile bull trout resighted per month after initial capture and marking. Marked individuals were resighted in the Skiphorton Creek study area (black bars), within 4 km of the study area (white bars), and >4 km away from the study area (hatched bars).

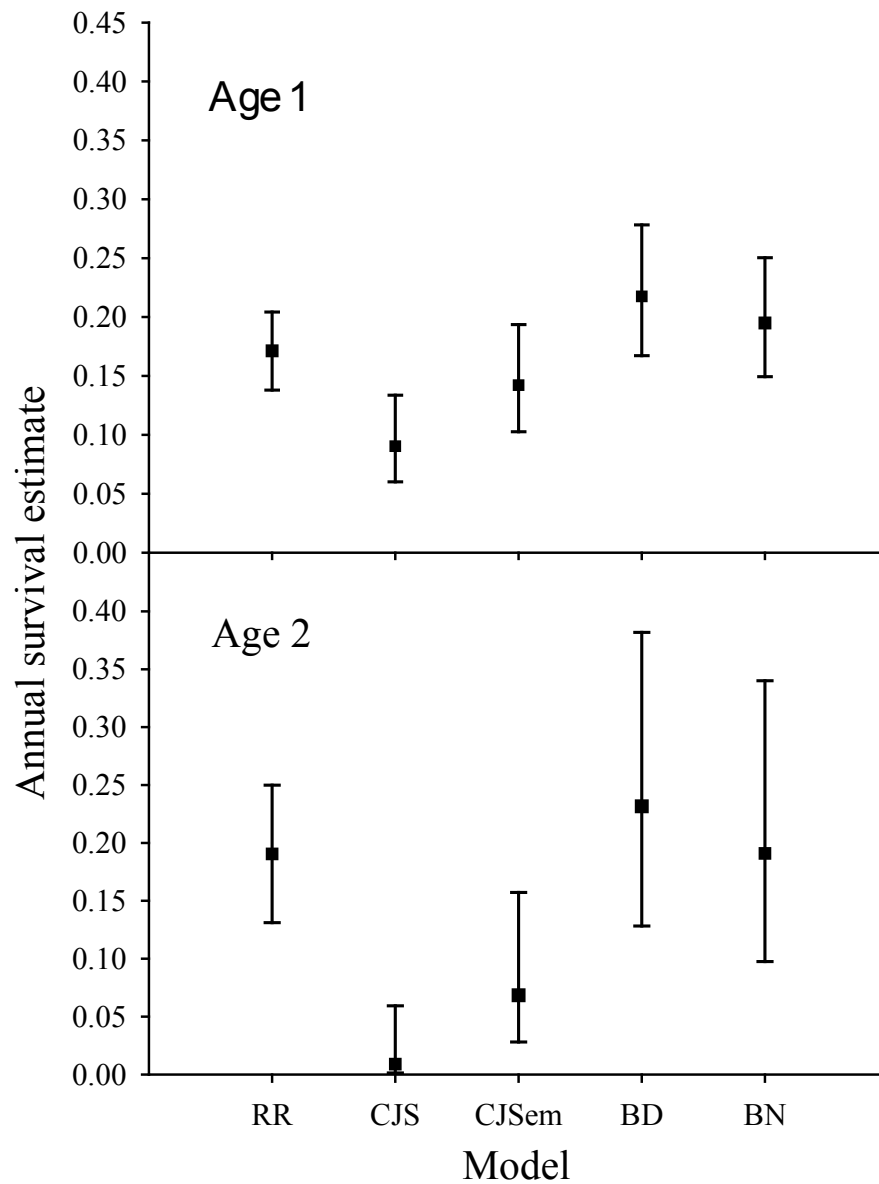


Figure 3.5. Estimates of survival probability for juvenile bull trout marked in Skipthorton Creek, Oregon, calculated using different methods: RR = return rate, CJS = naïve Cormack-Jolly-Seber, CJSem = ad hoc CJS with emigration included, BD = Barker model with dead recoveries, BN = Barker model without dead recoveries. Error bars represent 95% confidence intervals.

CHAPTER 4
CONSERVATION IMPLICATIONS OF MULTIPLE LIFE-HISTORY STRATEGIES
AND METAPOPULATION STRUCTURE IN A STREAM-DWELLING
CHAR, BULL TROUT⁴

Abstract

A variety of factors can limit the persistence of imperiled populations, including local processes that affect birth and death rates, as well as landscape-scale factors that influence interactions with other populations via immigration and emigration. We estimated life stage-specific demographic rates for threatened bull trout, and assembled stage-based population models to describe three representative life-history strategies. We evaluated the relative effect of changing individual demographic rates on long-term population growth rates of resident, migratory, and mixed life-history types. We then estimated empirical dispersal rates among individual populations and used these in a spatially realistic metapopulation model consisting of three bull trout populations. We simulated the effect of potential management and climate changes on survival, growth, and dispersal, and evaluated the associated effects on the probability of decline in abundance for individual populations and the metapopulation as a whole. All three bull trout life-history types were most sensitive to changes in juvenile survival rates, but the relative effect of changes in fertility and adult survival components varied among types. Changes in juvenile and subadult growth rates had marked effects on population trend for all life-history types. We observed infrequent dispersal of individual bull trout among distant patches (>70 km apart), from which we estimated low current rates of dispersal

⁴ Chapter co-authored with Tracy Bowerman, Phaedra Budy, and Howard Schaller

(<0.003). Dispersal rates across a range of values had little effect on overall metapopulation persistence, or the persistence of individual populations when all were declining. However, when population trends varied, dispersal helped buffer small or declining populations from extinction. When we evaluated three potential effects of climate change simultaneously, the response differed among life-history types, and the metapopulation response reflected the composition of life-history types within it. This research suggests that diversity in life-history strategies can help stabilize demographic responses to environmental perturbations, which may help decrease the risk of extinction for both individual populations and metapopulations. To provide as much demographic stability as possible, diversity within and among populations should be maintained along a continuum that emphasizes conservation of the full range of life-history traits expressed by bull trout.

Introduction

Conservation practitioners are often called upon to predict how populations will respond to management actions or environmental disturbances. Informed predictions require knowledge about local processes that affect birth and death rates, as well as landscape-scale factors that influence interactions with other populations via immigration and emigration. However, empirical estimates of specific demographic rates such as survival, fertility, and dispersal among populations are uncommon for many imperiled species, particularly those with multiple life stages and complex life histories (Heppell et al. 2000). When this information does exist, it can be used to populate detailed demographic models, which are valuable tools for endangered species recovery (Brook et al. 2000). Such models are often used to evaluate the relative contribution of specific

demographic processes to overall population growth and to assess extinction risks for imperiled populations (Doak et al. 1994; Hiraldo et al. 1996). For example, stage-structured demographic models have been used to analyze the cause of decline in whale populations (Fujiwara and Caswell 2001), and to identify management actions to aid recovery of endangered woodpeckers (Heppell et al. 1994). Evaluation of vital rates within the context of life-history variation can also help ecologists better understand how population structure and life-history expression might affect population growth. For example, populations composed mostly of resident versus migratory individuals may vary considerably in their response habitat loss (Bender et al. 1998).

Although management of endangered species often occurs at the population level, the long-term fate of many populations may ultimately depend on interactions with other populations (Brown and Kodric-Brown 1977). For species that occupy patchy or fragmented habitats, a complete understanding of factors limiting populations may entail evaluation of the connectivity among populations in addition to survival and reproductive rates within a population. The risk of extinction is often higher when populations are isolated, compared with when breeding individuals can move among populations (White 2000; Mills 2007). Conspecific populations that occupy discrete habitat patches and interact via dispersal can generally be defined as a metapopulation (Hanski and Gilpin 1991; Hanski and Simberloff 1997).

Salmonid fishes are among the many organisms that are thought to occur as metapopulations, and the spatial distribution of salmonid populations is an important consideration in conservation (Dunham and Rieman 1999; Gotelli 1999; Schtickzelle and Quinn 2007). Salmonids typically spawn in discrete patches of suitable habitat within a

river system and are known to show site fidelity to their natal spawning patch (Dunham et al. 2001a; Isaak and Thurow 2006), but may occasionally stray and reproduce in another patch (i.e., dispersal). Like many other mobile organisms, the occurrence of stream-dwelling fishes may be related to habitat patch size and degree of isolation (Rieman and Dunham 2000; Dunham et al. 2001a; Koizumi and Maekawa 2004), suggesting that connectivity plays an important role in population persistence (Fagan 2002). Despite the relevance of metapopulation theory to research on salmonid populations, the concept has not been widely applied (Schtickzelle and Quinn 2007). A lack of empirical studies on metapopulation dynamics may be due in part to the difficulty of obtaining accurate estimates of dispersal among populations (Nathan et al. 2003; Schtickzelle and Quinn 2007).

We compiled life stage-specific demographic rates for a threatened stream-dwelling salmonid, bull trout *Salvelinus confluentus*, to evaluate population-level responses to environmental perturbations and to assess the role of connectivity in maintaining bull trout metapopulations. Bull trout, a species of char native to the northwestern United States and Canada, have complex life cycles and exhibit multiple life-history strategies (Rieman and McIntyre 1993; McPhail and Baxter 1996). Bull trout are often categorized into two distinct life-history types, resident and migratory (Nelson et al. 2002; Howell and Sankovich 2012). Both resident and migratory life-history types spawn in cold headwater streams (Rieman and McIntyre 1993). Resident bull trout may spend their entire lives in natal rearing areas, where they grow slowly, and mature adults typically range from 140 to 300 mm in fork length (FL; Goetz 1989; Hemmingsen et al. 2001; Howell and Sankovich 2012). In contrast, migratory bull trout may remain in

headwater streams with residents for several years before moving as far as 200 km downstream into larger rivers (fluvial life-history strategy), lakes (adfluvial strategy), or the ocean (anadromous strategy; Brenkman and Corbett 2005; Fraley and Shepard 1989). Migratory individuals generally overwinter in larger water bodies, and move upstream into headwater streams between June and October to spawn. Migratory bull trout typically mature at sizes greater than 300 mm FL and can exceed 800 mm FL (Goetz 1989; Johnston and Post 2009).

Despite general differences in behavior, growth, and size at reproduction among life-history types, the degree of life-history separation is more ambiguous in many systems where migration timing and distances can be highly variable (Downs et al. 2006; DuPont et al. 2007; Homel and Budy 2008). Growth rates and maturation timing can also differ greatly among individuals within a single system, as well as among populations (Al-Chokhachy and Budy 2008). This variability has led some researchers to suggest that life-history traits in bull trout can occur along a continuum, and that populations are likely to be composed of individuals that express different life-history strategies (Homel and Budy 2008; Homel et al. 2008). Due to the diversity in bull trout behavior and biology, as well as the wide range of habitat used throughout the life cycle, well-informed management decisions rely on a complete understanding the influence of specific demographic rates on overall population growth rate, particularly within the context of life-history variation (Johnston et al. 2007).

On a larger spatial scale, conservation of bull trout populations will benefit from an understanding of how populations interact from both genetic and demographic perspectives. Bull trout are extremely philopatric, and genetic research indicate low rates

of interbreeding between populations (Leary et al. 1993; Ardren et al. 2011). However, patterns of occurrence suggest that bull trout exist as metapopulations, with migratory corridors in large, mainstem rivers connecting isolated spawning habitat patches located in headwater streams (Dunham and Rieman 1999). Current knowledge of dispersal rates between spawning habitat patches and the effect of dispersal on metapopulation dynamics is extremely limited. A greater understanding of how populations interact via dispersal, and the effect of physical barriers on those dispersal patterns, will help guide management of migratory corridors and define the spatial scale at which bull trout conservation should be considered.

To characterize the diversity in bull trout demography, we developed stage-based models to represent a range of life-history characteristics exhibited by different bull trout populations. We used these models to explore possible effects of natural or anthropogenic factors that influence particular portions of habitat or specific life stages, and evaluated the population-level and metapopulation response to such changes (Figure 4.1). The intent of this study was to use available data on bull trout demographic rates to characterize populations and to explore potential effects of environmental changes on bull trout population viability. Within this framework, we had four primary objectives. Our first objective was to develop life-stage-specific demographic models based on empirical vital rate estimates to describe different bull trout life-history types. Second, we assessed the relative sensitivity of bull trout populations to changes in specific demographic parameters. To evaluate the importance of stream connectivity for bull trout, our third objective was to estimate dispersal rates among populations and use this to model metapopulation processes. Finally, we evaluated some potential responses of a

metapopulation to changes in dispersal, survival, and growth rates that might result from management actions or climate change.

Methods

Primary data sources and study area

We developed demographic models to describe individual populations and a combined metapopulation based on data from three bull trout populations within the Walla Walla River basin, located on the border of Oregon and Washington: the South Fork of the Walla Walla River (SFWWR), Mill Creek (MC), and the Touchet River (TR; Figure 4.2). Spawning and rearing for each population occurs in headwater tributaries to the Walla Walla River, and these headwater areas are considered distinct spawning habitat patches (Dunham et al. 2001a; Rieman and McIntyre 1995).

Prior to this study, bull trout from all three populations had been observed migrating throughout the Walla Walla basin, but rates of dispersal among individual populations had not been quantified (Anglin et al. 2008). Genetic comparisons among populations in the basin suggest low levels of genetic exchange (Kassler and Mendel 2007). As such, we hypothesized that bull trout populations within the Walla Walla basin effectively operate as a metapopulation with limited dispersal among all three populations. Current rates of movement and survival throughout the basin may be lower than historic rates due to habitat degradation in migratory corridors in the form of dams, low streamflow during summer months, channel homogenization, and other anthropogenic changes concentrated in lower portions of the watershed.

We estimated vital rates for the population models based on ten years of capture-mark-recapture (CMR) data from the MC and SFWWR populations. In both systems, we marked bull trout with unique passive integrated transponder (PIT) tags, and subsequently recaptured fish via systematic sampling and at several trapping locations (Figure 4.2). We collected additional resight data at stationary passive in-stream antennas (PIAs) located throughout MC, SFWWR, and the mainstem Walla Walla River (more detailed descriptions of the system can be found in Howell and Sankovich 2012 and Al-Chokhachy and Budy 2008). We used both active recaptures and passive resights of marked fish to inform vital rate estimates, and henceforth refer to a combination of the two as “detections.”

To represent the complex life cycle of bull trout given the amount of available data, we defined seven life stages based on a length-at-age relationship for bull trout (Table 4.1; see Appendix B for details describing the length-at-age relationship). Based on data from the SFWWR bull trout population, stages corresponded approximately with age. We determined the composition of life-history types for each of the three populations in the WW watershed according to the percentage of marked individuals exhibiting migratory traits and behavior. The population of bull trout in MC is considered mostly migratory, as females typically mature at lengths greater than 300 mm FL and large mature females (e.g., >300 mm FL) have not been observed in spawning areas outside of the spawning season (Howell and Sankovich 2012). In contrast, the SFWWR population is comprised of both migratory and resident bull trout. Large adults exceed lengths of 700 mm total length (TL) and many make long spawning migrations, while others mature at small sizes (200 mm TL) and are not observed downstream of

spawning areas (Al-Chokhachy and Budy 2008; Homel and Budy 2008). Monitoring data suggests that the SFWWR bull trout population is composed of approximately 70% fish that exhibit migratory behavior at some stage in their life cycle, and 30% that do not (Budy et al. 2010). To maintain consistent terminology, we called this combination of both migratory and resident life-history strategies a "mixed" life-history type (LHT). Observations of fish size and movement suggest that the TR population is also a mixed LHT (Mendel et al. 2003), but because the proportion of fish exhibiting migratory versus resident behavior is unknown, we used the same mixed LHT model developed for the SFWWR population to also describe the TR population.

Vital rate estimates

We used data from MC and SFWWR bull trout populations to estimate the number of eggs per female, spawning probability, and growth and survival rates for each life stage. We established a standardized relationship between female length and number of eggs from 22 sacrificed mature females between 205 and 674 mm TL. We then determined the number of eggs per female for each life stage based on the median length of each stage (Morris and Doak 2002). We estimated stage-specific spawning probabilities from the ratio of marked fish in each stage that made a spawning migration relative to the total number of marked fish that were detected anywhere in the watershed in a given year. That is, if individuals moved upstream into spawning areas during the summer and downstream in the fall, we considered that a spawning migration (although we could not determine if individuals spawned successfully). We compared the number of fish that exhibited this spawning pattern with the number of fish that were detected during that same year but showed no clear seasonal movement pattern. Estimates of

spawning probability for resident fish were unavailable in the literature, so we so we assumed spawning probabilities similar to those observed for migratory fish, adjusted to describe a population that can reach sexual maturity at 140 mm FL and where individuals typically do not exceed 300 mm FL (Rieman and McIntyre 1993; Howell and Sankovich 2012). Observations of the number of redds compared to the number of mature females in a nearby resident population supported this assumption (Moore et al. 2006).

To estimate stage transition rates, we calculated the proportion of marked survivors from a given stage during one year that grew into another stage in the following year (Morris and Doak 2002). Due to low sample size, we combined annual recapture data from all ten years of the study. We estimated transition rates for all stages of the SFWWR population, but data were unavailable for several stages in both the TR and MC populations. As such, we used estimates of stage-5 and -6 transition probabilities from the MC population to describe transition rates for the migratory LHT, and estimates from the SFWWR as a baseline for all other life stages in both mixed and migratory demographic models. To represent slow growth rates exhibited by the resident LHT, we assumed much lower transition probabilities for all stages except stage 1, when all three LHTs occupy the same habitat.

We estimated survival rates for each of the six largest size classes (stage 2 through stage 7+) from 10 years of CMR data in the SFWWR. We used the Barker model implemented in Program MARK (White and Burnham 1999) to estimate mean survival over time for each of the stages, which we modeled as separate groups. We applied Markov Chain Monte Carlo simulations within a Bayesian framework to analyze a random effects model, with survival estimated on the logit scale and time treated as a

random effect (White et al. 2009). We used minimally informative prior distributions for all parameters and retained 10,000 samples from the posterior distribution to estimate the mean survival rate and temporal process variance for each of the six stages (see Appendix B for details). A variance components approach is the preferred method for estimating vital rates in a population viability analysis, as it should provide the least biased estimates of mean survival, as well as isolate process variance from sampling variance (White 2000). We used mean estimates of survival from this analysis in all population models. We used estimates of process variance (σ^2) in stochastic models to represent biological variation due to temporal differences in survival.

We did not have enough years of data to estimate survival of stage-1 bull trout in the same manner, so we used estimates from the literature (see Chapter 3, this volume). These estimates were based on only 3 years of data, so temporal variance was not estimable. We therefore used the same estimate of variance from the next larger stage ($\sigma = 0.205$), as survival rates were similar between these two size classes (Chapter 3, this volume).

Life-history-specific demographic models

We used vital rates described above to develop a stage-based, pre-breeding Lefkovitch matrix model to describe the bull trout life cycle that represented only the female portion of the population (Figure 4.3; Caswell 2001). Initially, we developed a life-cycle model to describe the mixed LHT of the SFWWR population, for which we had empirical estimates to describe nearly every life-history parameter. We then altered parameters within the model to represent what we know about resident and migratory life-histories (Rieman and McIntyre 1993; Howell and Sankovich 2012), and included

vital rate estimates from the migratory MC population where possible. In the model for the migratory LHT, individuals matured in stage 5 (> 300 mm TL), had high transition probabilities corresponding with rapid growth rates (e.g., $50\text{-}120$ mm \cdot year $^{-1}$), and could reach ages 10 or older (Figure 4.3). The mixed LHT model described a population in which individuals matured between stages 2 and 6, transition probabilities were intermediate, and individuals could reach ages of 8 to 10 years. In contrast, the resident LHT matured as early as stage 2 (> 155 mm TL), had low transition probabilities (e.g., growth rates of 15 to 50 mm \cdot year $^{-1}$), rarely exceeded 300 mm TL, and reached ages of 8 to 10.

In this study, we wished to develop a model representative of a population with decreasing abundance, as has been observed in bull trout populations of concern (Rieman et al. 1997). We developed base models with a declining population growth rate (λ), where $\lambda = 0.931$, a recent estimate based on seven years of CMR data from the SFWWR population (Budy et al. 2010). To represent declining populations, we developed models with conservative levels of survivorship and growth, relative to other estimates in the literature (Pratt 1992; Al-Chokhachy and Budy 2008). Survival and growth probabilities were represented in the matrices by P_i , the probability of surviving and staying in the same stage the following year, and G_i the probability of surviving and moving to the next stage such that $P_i = \hat{s}_i(1 - \hat{\gamma}_i)$ and $G_i = \hat{s}_i\hat{\gamma}_i$, where \hat{s}_i is the survival probability and $\hat{\gamma}_i$ is the probability of an individual transitioning from stage i to $i+1$ (Caswell 2001). Because temporal variance was associated with \hat{s}_i , we apportioned variance between the two survival parameters by multiplying P_i and G_i by the coefficient of variation (CV) associated with each \hat{s}_i (Morris and Doak 2002). All three LHT models included the

same estimates of stage-specific survival, but for all stages beyond stage 1, transition rates were greater for the migratory LHT, and considerably lower for the resident LHT, resulting in different estimates of P_i and G_i . Estimates for the mixed LHT were representative of a population with approximately 70% migratory and 30% resident individuals.

We estimated the fertility rate as the number of female offspring produced by a mature female bull trout in each stage i that survived to stage 1, as

$$F_i = m_i B_i R S_{egg} S_0,$$

where m_i (fecundity) indicates the average number of eggs produced by a female of the median length for each stage i , B_i is the probability of spawning for a female in stage i , R is the ratio between sexes (assumed 0.5), S_{egg} is the probability of survival between egg deposition and fry emergence, and S_0 is the probability of survival from fry emergence to stage 1 (70 mm TL). We used data from an experiment which evaluated bull trout egg survival in a natural stream to estimate S_{egg} based on the mean egg-to-fry survival rate for eggs reared in incubation capsules in which the sediment composition approximated that of the surrounding redd, as we expected these estimates to be the most representative of natural conditions (Chapter 2, this volume). Estimates of age-0 survival are lacking for bull trout, so we back-calculated this vital rate after all other life stages had been assembled in the population matrix (Morris and Doak 2002). We set the dominant eigenvalue (the asymptotic population growth rate) equal to $\lambda=0.931$ and solved for the unknown parameter, S_0 . To assess the validity of S_{egg} and S_0 estimates, we compared them with estimates for other salmonid species in the literature. We assumed consistent

rates of S_0 and S_{egg} among the three LHTs, and only m_i and B_i varied among types according to size and length at maturity.

Asymptotic sensitivity analyses

To evaluate the relative effect of changes to individual vital rates on overall population growth rates among the three LHTs, we calculated elasticity and sensitivity values for each, based on an asymptotic λ , assuming a stable stage distribution. Elasticities describe the proportional change in λ resulting from a proportional change in each vital rate independently (Caswell 2001). Elasticity values account for the differences in scale between survival probabilities and fertility rates, and provide a means to assess the relative effect of changes to a single vital rate on the overall population growth rate (Heppell et al. 2000). The sensitivity of λ with respect to a change in an individual vital rate describes the absolute change in the finite rate of population growth resulting from a change in a given vital rate. To examine sensitivity values, we estimated λ across the range of each vital rate (from 0 to 1 for probabilities and from 0 to 200 for fertility values), while holding all other vital rates constant (Morris and Doak 2002). This sensitivity analysis allowed us to evaluate λ within a range of biologically feasible values of each vital rate and assess nonlinear responses in λ to changes in vital rates. We also compared the change in λ relative to specific matrix elements among the three LHTs.

Dispersal rate estimation

Dispersal events for bull trout are infrequent and thus difficult to observe, resulting in a paucity of true long-distance movement and dispersal data (Dunham and Rieman 1999; Nathan et al. 2003). We therefore compared estimates of dispersal based

on empirical data to a more general dispersal kernel and to a metric of genetic exchange between populations. This comparison helped us validate our observations, and genetic information allowed us to assess the assumption that movement from one patch to another represented successful dispersal.

First, we estimated dispersal rates based on mark-recapture observations of individuals marked in one spawning patch that were later detected in a different patch during the spawning season. We then calculated a rate by comparing this number to the total number of marked individuals detected again anywhere in the Walla Walla basin. We compared these dispersal rate estimates to estimates generated from a dispersal kernel that models a decrease in the probability of successful dispersal as the distance between populations increases (Fullerton et al. 2011; Schick and Lindley 2007). The dispersal kernel can be described by

$$M_{ij} = \frac{1}{2\alpha} \exp\left(\frac{-D_{ij}}{\alpha}\right),$$

where M_{ij} represents the probability of an individual dispersing from spawning patch i to patch j , α is the maximum dispersal distance (150 km), and D_{ij} is the linear stream distance in km between the two spawning patches.

We also used a genetic approach to assess the relative degree of connectivity among populations in the Walla Walla basin based on an indirect metric of gene flow described as the average number of migrants per generation. We used pairwise F_{st} values estimated from 15 microsatellite loci from individuals in each of the three Walla Walla basin populations (Kassler and Mendel 2007) to assess the average number of migrants per generation (Nm ; i.e., successful dispersers). Assuming the island model of migration (Allendorf and Luikart 2007),

$$N_m \approx \frac{1-F_{st}}{4F_{st}} .$$

As F_{st} is a measure of allele frequency divergence among subpopulations, pairwise F_{st} values are likely to reflect both current and historic gene flow (Mills 2007). For this reason, and because estimation of N_m hinges upon a number of assumptions, these estimates should not be viewed as direct measures of dispersal, but rather can be used as a relative assessment of long-term genetic interaction between populations (Allendorf and Luikart 2007; Mills 2007).

Population capacity based on spawning habitat

Many populations are regulated by density dependent factors, which limit population growth as abundance increases, and it is important to include such biological limitations in population models (Ginzburg et al. 1990). However, for most bull trout populations, there are insufficient data with which to estimate a carrying capacity (but see Johnston and Post 2009). To represent territoriality exhibited by bull trout and limitations on available spawning sites, we established a carrying capacity function to approximate the maximum potential number of redds in each spawning patch based on physical habitat attributes and used this as a ceiling function in population models (Figure 4.1). First, we used 16 years of redd count data from the three Walla Walla bull trout populations (Mahoney et al. 2011) to designate stream reaches in one of four spawning habitat categories based on average redd densities: no spawning, low density mainstem, high density mainstem, and spawning tributaries. Next, for all stream kilometers within the Walla Walla basin, we compiled physical habitat characteristics estimated from 1:24,000 hydrography provided by StreamNet and summarized in Mobrand Biometrics' Ecosystem Diagnosis and Treatment (EDT) analysis (see <http://www.nwcouncil.org/edt/>

for data and additional information). All environmental variables were taken directly from the Stream Reach Editor and applied in GIS at the scale of stream reaches, which ranged from 0.1 to 8 km in length.

We used classification and regression tree (CART) analysis in the tree package in R 2.13.0 (Ripley 2012) to evaluate the relationship between spawning habitat category and predictive environmental variables. We evaluated habitat variables that had previously been associated with bull trout distributions, such as elevation, channel slope, and maximum summer temperature (McCleary and Hassan 2008; Wenger et al. 2011). We also included variables that we hypothesized might affect spawning habitat availability at a smaller spatial scale (e.g., percent pools, scour). We used results from the CART analysis to establish discrete break-points for continuous predictor variables (e.g., elevation) and to define a rule set for each of the spawning habitat categories based on physical habitat measurements. We applied the rule set to the entire Walla Walla basin to predict the total amount of spawning habitat in each category in each of the three spawning patches. We also calculated the length of stream within each category in spawning survey index reaches (the portions of each spawning habitat patch where spawning surveys are conducted annually to evaluate population trend). We used the 90th percentile of redd densities observed in each spawning habitat category as the redd capacity for that category. We then estimated the maximum number of redds (total spawner capacity; K) expected for the spawning index reaches within each patch based on

$$K = \sum_h^n (L_h * D_L),$$

where L indicates the length of a stream reach, D is the maximum spawning density, and h represents the specific habitat type (Bartz et al. 2006).

Stream temperature change

Based on recent evidence of widespread stream temperature increases over the past two decades in the Western U.S., and the potential for accompanying shifts in species distributions (Isaak et al. 2011), we assessed potential changes to available bull trout habitat within the Walla Walla basin as a result of stream temperature warming (Figure 4.1). We used water temperature measurements taken at four different sites along the profile of the SFWWR to estimate a stream temperature lapse rate, or the average rate of temperature change along the elevational gradient of a stream ($^{\circ}\text{C} \cdot 100 \text{ m}^{-1}$ elevation increase; Isaak and Rieman 2013). We then used the stream lapse rate of $0.5 ^{\circ}\text{C} \cdot 100 \text{ m}^{-1}$ calculated for the SFWWR in conjunction with channel slope and projected long-term rates of stream warming to estimate the rate at which stream temperatures could gradually increase along the longitudinal profile of the stream. The expectation is that as water temperatures increase, the physical location representing a particular temperature threshold will track upward in elevation (Isaak and Rieman 2013). We predicted the rate at which this temperature boundary, or stream temperature isotherm, would shift in the upstream direction based on an equation from Isaak and Rieman (2013):

$$ISR = (\text{stream warming rate}/\text{lapse rate})/\sin(\text{channel slope}),$$

where ISR is the isotherm shift rate (km/decade). We evaluated potential ISRs based on a range of long-term stream warming rates ranging from 0.1 to 0.3 $^{\circ}\text{C}$ per decade and for a range of channel slopes. Changes in stream temperature of this magnitude are

consistent with those observed in western streams over the past three decades (Isaak et al. 2011).

To apply stream warming rates to capacity function predictions, we assumed that current downstream spawning and rearing distributions for bull trout are currently limited by a critical temperature threshold represented by a temperature isotherm. As stream temperatures warm, we assumed that the downstream boundary of bull trout distributions will move upstream at the rate predicted by the ISR equation, depending upon channel slope. We applied ISRs estimated from the SFWWR to the known distribution of spawning habitat in all three patches within the Walla Walla basin, based on an average stream slope of 2% and 3% for low and high density mainstem habitat, respectively, and 5% for spawning tributary habitat (stream slope data from EDT analysis, Mobrand Biometrics). We used ISRs to predict how far upstream a temperature isotherm could move over the next 25 years. Under the assumption that bull trout distributions will track the temperature isotherm, we estimated the changes in stream length available for spawning within the three patches and within spawning index reaches only. As bull trout distributions appear to be limited by stream size in the upper portions of stream systems, isotherm shifts resulted in habitat loss. Based on these new estimates of available habitat, we then predicted the change in total spawner capacity based on index reaches in the MC, SFWWR, and TR populations over the next 25 years. We modeled population change over a 25 year time span because this is the time frame over which many temperature models are more accurate, and because it is a time frame relevant to many management decisions.

Metapopulation viability assessment

We developed a spatially explicit metapopulation model composed of three distinct bull trout populations within the Walla Walla basin (Figure 4.1). We used the mixed LHT model used to describe the SFWWR and TR populations and the migratory LHT model to describe the MC population. We estimated the initial abundance for each population based on the average number of redds counted during annual surveys of index reaches in each of the three spawning patches between 1996 and 2008 (Figure 4.2). To produce initial population vectors, total spawner abundance was distributed among stages according to the stable stage distribution multiplied by the probability of spawning for each stage. As such, initial population sizes in simulations represented the number of breeding females in spawning survey index reaches only. We used this metric in metapopulation simulations because redd counts are a common measure of bull trout population abundance and trend (Dunham et al. 2001b; Al-Chokhachy et al. 2005), and because changes in spawner abundances would not be observed unless they occurred within index reaches.

We projected future population size with an annual time step based on

$$N_{i(t+1)} = \mathbf{A}N_{i(t)} - \sum M_{ji}N_{i(t)} + \sum M_{ij} N_{j(t)}$$

where \mathbf{A} is the population projection matrix, and $N_{i(t)}$ is a vector of abundances of individuals in each life stage in population i in one year, $N_{i(t+1)}$ is the abundance in each stage of the population in the following year, $\sum M_{ji}N_{i(t)}$ is the total number of dispersers emigrating from patch i to all other populations j , and $\sum M_{ij} N_{j(t)}$ is the total number of dispersers immigrating into patch i from all other patches j . Dispersing individuals were

drawn only from reproductive adult stages (stages 5 through 7), as only reproductive migratory adults were assumed to disperse.

For population simulations, we assumed a declining growth rate of $\lambda = 0.931$ in the base model for all populations, and as such, we considered future projections conservative, or worst-case, outcomes. Based on population trend data, this asymptotic growth rate may represent the gradual decline reported in many bull trout populations (Rieman and McIntyre 1993; Rieman et al. 1997). For all scenarios, we included demographic stochasticity by sampling the number of survivors and dispersers from binomial distributions, and the number of age-1 individuals produced at each time step from a Poisson distribution (Akçakaya 2000). We also included environmental stochasticity by sampling survival probabilities from a normal distribution based on estimated mean and variance (σ) for each life stage from our survival analysis, and sampled fertility probabilities from a normal distribution with a mean estimate for each stage, and a naïve estimate of variance ($\sigma = 0.1$). We used estimates of maximum spawning capacity as a ceiling for adult abundance in each population, but because we were modeling populations with a long-term declining trend, we did not include other density-dependent effects (Ginzburg et al. 1990). We projected each scenario over 25 years to estimate the probability of the metapopulation declining by a percentage of its current size. We ran 1,000 simulations of each scenario and included variance for each matrix parameter to model environmental stochasticity.

We ran a series of stochastic population simulations in the program RAMAS Metapop to evaluate the potential effects of dispersal rates, management actions, and climate change on long-term persistence of the three individual populations within the

Walla Walla basin and the metapopulation as a whole (Figure 4.1). We investigated the hypothesized effect of two management actions: (1) increased survival of stages 3 and 4 by 10% of current values to represent improved subadult feeding and rearing habitat, and (2) increased survival of the two largest stages by 10% as a result of improved passage conditions (e.g., removal of barriers to facilitate migration between habitats). We also hypothesized three potential effects of climate change on vital rates.

First, we modeled a decrease in survival of bull trout eggs and alevins by 20% of current estimates to simulate increased scour or sedimentation of redds during embryo development as a result of an earlier peak in the hydrograph (Mantua et al. 2010; Shellberg et al. 2010; Chapter 2, this volume). Second, we increased juvenile bull trout growth rates by 10% of current rates based on the hypothesis that increased temperatures in headwater areas would be more optimal for growth, assuming that stream productivity also increased concurrently (Zuo et al. 2012). Third, we decreased subadult growth rates by 10% under the hypothesis that warmer water temperatures in lower-elevation rearing areas would increase past optimal temperatures for growth. These assumptions were based on bioenergetic measurements of optimal growth and consumption relative to water temperature (Selong et al. 2001; Mesa et al. 2013). To incorporate changes in growth into our models, we altered individual growth rate measurements from recapture data by the specified percentage and then re-calculated transition probabilities. We also ran scenarios in which we combined all climate and management scenarios simultaneously. Percent changes to vital rates represented modest modifications within the 95% confidence intervals of all estimated rates.

To evaluate the effect of dispersal rates on population persistence, we calculated the probability of decline for each of the three populations within the Walla Walla basin, and the metapopulation as a whole, under two different possible scenarios. First, we increased the rate of dispersal between 0 and 0.1 for the base model (all three sub-populations declining; $\lambda = 0.931$). Next, we evaluated the effect of the same range of dispersal rates given a scenario in which all populations were subject to the combined effects of climate change (decreased egg survival and subadult growth, and increased stage-1 growth). In the latter scenario, management actions were applied to the SFWWR and TR populations ($\lambda = 0.983$), but not to the MC population ($\lambda = 0.927$). Dispersal rates were selected to represent a range of migration gradients ranging from populations that are completely isolated, to populations with a very high degree of connectivity (10% of adults in each population disperse).

Results

Bull trout vital rates

Sexually mature fish examined in the SFWWR ranged from 205 to 674 mm TL, and the oldest fish aged was 10 years old (supplementary material Figure B.1). The relationship between female length and the number of eggs was described by

$$N_{eggs} = 0.0084TL^{2.032},$$

where N_{eggs} is the number of eggs per female, and TL is total length in mm (supplementary material Figure B.2). Based on this relationship, the predicted number of eggs per female of the median size in each class ranged from 227 for stage 2, to 3184 for a 550 mm TL fish (Table 4.2). As there was no terminal length for the largest stage, we

estimated the number of eggs for stage 7 based on the average length of captured fish larger than 420 mm in the SFWWR (500 mm TL) for the mixed LHT, and we assumed a slightly larger median size for the migratory LHT (550 mm TL).

In the SFWWR, we observed 124 fish that made distinct spawning migrations, most of them on consecutive years. The proportion of bull trout that made a spawning migration relative to the number detected ranged from 0.05 for stage 3 to 0.7 for stage 7 (Table 4.1; Supplementary material Table B.2). We considered these estimates conservative owing to incomplete detection probability of migrants and a bias against observing spawning migrations for resident fish. As research suggests that the majority of bull trout in many systems spawn annually (Downs et al. 2006; Johnston and Post 2009; Budy et al. 2010), we used our observations as a conservative baseline for model simulations and increased the spawning probability to 0.9 for the largest stages (Table 4.2).

Annual growth rates for fish recaptured throughout the Walla Walla basin varied greatly among stages, locations, and individual fish. Growth rates ranged from no change in length to an increase of 106 mm in a year (66% of initial length). Growth rates were typically greatest for stages 3 through 5, but there was substantial variability within and among stages, and among populations (supplementary material Figure B.3). Data from the SFWWR showed that the majority of fish in stages 1 through 4 transitioned into the next stage each year, whereas fish were more likely to remain in stages 5 and 6 for more than one year (Table 4.1; Appendix Table B.3a). Compared with observations from the SFWWR, recaptured adult bull trout in MC exhibited higher average growth rates and were more likely to transition from stages 5 and 6 into larger stages each year (Table 4.1;

Appendix Table B.3b). The probability of a fish in stage 5 transitioning into stage 6 the following year was 0.3 in the SFWWR compared with 0.83 in MC, and the transition probability from stage 6 to 7 was 0.2 in SFWWR compared with 0.76 in MC.

Mean estimates of annual survival rates across ten years indicated that survival generally increased as bull trout got larger, ranging from estimates of 0.26 for stage-2 fish to 0.47 for stage-7 fish (Table 4.1). Annual survival estimates varied among years, but were the most consistent for stages 5 and 6, and the most variable for stages 2 and 7 (Table 4.1; AppendixTable B.4). Estimates of temporal process variance (σ) ranged from 0.048 to 0.205, with the highest estimates of variance for stages 2, 4, and 7 (Table 4.1; Table B.4).

Sensitivity of population growth rate to changes in vital rates

The relative contribution of individual vital rates to overall population growth varied among migratory, mixed, and resident life-history types. For all three LHTs, matrix elements representing subadult survival and transition (G_1 and G_2 for all types, in addition to G_3 and G_4 for the migratory LHT) had the highest elasticity values, indicating that survival of pre-reproductive life stages had the greatest proportional contribution to overall population growth (Figure 4.4). Fertility and survival elasticity values for the largest stage were the highest for the migratory type compared with the other LHTs, demonstrating a greater relative contribution of large individuals to overall population growth. In comparison, elasticity values for fertility and the probability of surviving in remaining in the same stage were the highest in stages 2 and 3 for the resident LHT because of slow growth rates and early size at reproduction (Figure 4.4). Elasticity values were relatively more uniform among fertility and adult survival matrix elements

for the mixed LHT, reflecting a population structure in which survival and fertility were more evenly distributed across numerous life stages (i.e., more life stages contributed to offspring compared with other LHTs).

Elasticity values represent a proportional change in λ resulting from a proportional change in a vital rate and as such, can be summed together to evaluate the total contribution of a portion of the life cycle. When we summed elasticity values across stages, juvenile survival had the largest proportional contribution to population growth for all LHTs compared with adult survival and fertility (Figure 4.5). However, among LHTs, fertility had the greatest influence on λ for the resident LHT, whereas adult survival had the greatest influence on λ for the migratory LHT. Once again, elasticity values for fertility and adult survival for the mixed LHT was intermediate between the other two.

For each of the LHTs, we illustrate the relative effect of changing representative individual matrix elements on population growth rates across a range of values while holding all other matrix elements constant (Figure 4.6). A line with a steeper slope indicates a greater response of λ to changes in a matrix element. For example, although values of juvenile survival (G_1) were equivalent for all population types, a stable population growth rate ($\lambda = 1$) could be reached by increasing G_1 to 0.27 (27% increase) for the resident LHT, to 0.30 for the mixed LHT (43% increase), and to 0.34 for the migratory LHT (62% increase; Figure 4.6 upper panel). In comparison, increased survival of the largest adult stage (largest P) would have a relatively greater influence on λ for the migratory population (Figure 4.6 lower panel). In both examples, the response of the mixed life-history type fell between that of the migratory and resident. Exploring

sensitivity values in this manner also demonstrates that increased survival within the 95% credible intervals for the largest stages would not be sufficient for any of the three LHTs to reach a stable population growth rate ($\lambda \approx 1$).

Dispersal rates between populations

Over a ten year period, we observed 33 marked bull trout migrate distances greater than 70 km, and 9 fish traveled farther than 100 km. During this time, two marked individuals from the MC population made spawning migrations into the SFWWR population, and one individual from the TR population migrated into the MC population during spawning. We considered each of these fish successful dispersers. Based on the total number of marked fish that were resighted during the study, the proportionate estimate of dispersal was 0.0052 from MC to SFWWR, and 0.0098 from TR to MC over a 7-year period (Table 4.3a).

Dispersal rates calculated using the dispersal kernel function were 0.0021 between MC and SFWWR populations, 0.0014 between SFWWR and TR, and 0.0015 between MC and TR (Table 4.5b). These dispersal rates were based on distance between spawning patches, and thus, the same rate applied in both directions, even though the potential for dispersal may be greater in one direction than the other.

Based on the general metric from pairwise F_{st} values, we estimated approximately 4 migrants per generation between SFWWR and MC, 3 between SFWWR and TR, and 2 between MC and TR (Table 4.3c). As with the distance function, direction of travel could not be inferred. All three metrics of connectivity suggested similarly low levels of dispersal (e.g., approximately 2 to 6 individuals per generation) among the three populations of bull trout in the Walla Walla basin.

Carrying capacity of spawning habitat

The best predictors of bull trout spawning habitat type were elevation, stream gradient, stream width, and maximum summer temperature. The CART model that included the first three variables had an 86% overall classification success rate, and we included maximum summer temperature post-analysis to distinguish between the remaining sites where spawning had been observed (Table 4.4). In the Walla Walla basin, bull trout spawned at elevations above 700 m, and no spawning was observed where stream gradients exceeded 7.45%. These criteria defined the lower and upper boundaries of most spawning areas in the watershed, respectively. Stream gradient was an important criterion for categorizing all habitat types, and width was used to distinguish between small tributaries and high density mainstem habitat. Based on the defined rule set, we estimated a total of 45 km of spawning habitat in the SFWWR, 22 km in MC, and 43.7 km in the TR under current conditions (Figure 4.7 left panel; Table 4.5b). When only the spawning survey index reaches were considered, total available stream length was 11.9, 17.6, and 22.0 km for the three respective populations (Table 4.5c). The current estimated maximum redd capacity estimated in index reaches was 478 for the SFWWR population, 395 for the MC population, and 690 for the TR population (Table 4.5d).

Stream isotherm shifts and predicted loss of spawning habitat

According to one recent study, streams in the interior Columbia Basin have been warming at a rate of approximately $0.17\text{ }^{\circ}\text{C}\cdot\text{decade}^{-1}$ over the past 20 years (Isaak et al. 2011). Based on this rate of warming, we estimated isotherm shift rates of between 1 and $1.6\text{ km}\cdot\text{decade}^{-1}$ for spawning habitat in the Walla Walla basin, for reaches with channel

slopes of 3 and 2%, respectively, and $0.63 \text{ km} \cdot \text{decade}^{-1}$ for streams with a 5% slope ($0.15 \text{ }^{\circ}\text{C} \cdot \text{decade}^{-1}$; Table 4.5a). Under projected accelerated stream warming rates of 0.2 to $0.3 \text{ }^{\circ}\text{C} \cdot \text{decade}^{-1}$, isotherms could shift upstream as rapidly as 2 to $3 \text{ km} \cdot \text{decade}^{-1}$ in spawning areas with 2% slopes, and 1.4 to $2 \text{ km} \cdot \text{decade}^{-1}$ for stream sections with 3% slopes. Isotherms in bull trout spawning tributaries with steeper slopes (e.g., 5%) would likely shift more slowly (0.8 to $1.25 \text{ km} \cdot \text{decade}^{-1}$).

When we applied isotherm shift rates to current spawning habitat distributions in the Walla Walla basin, we estimated a loss of 6.6 km of spawning habitat over the next 25 years in SFWWR, 5.8 km in MC, and 14 km in the TR under current rates of stream warming (Table 4.5b). If stream temperature warming accelerates to $0.2 \text{ }^{\circ}\text{C} \cdot \text{decade}^{-1}$, in 25 years, spawning habitat could be reduced by as much as 8.7 km in SFWWR, 8.2 km in MC and more than 12.1 km in the TR (Figure 4.7 right panel). When we assessed changes to spawning habitat index areas with a forecasted $0.2 \text{ }^{\circ}\text{C} \cdot \text{decade}^{-1}$ rate of warming, the amount of available spawning habitat did not change in the SFWWR, as spawning index sites were located 13 km upstream of the current downstream spawning distribution (the location of the baseline isotherm). Predicted available habitat was reduced by 6 and 12 km for the MC and TR populations, respectively (Table 4.5c). Based on our estimates of maximum density in spawning index reaches, the loss of spawning habitat associated with a $0.2 \text{ }^{\circ}\text{C} \cdot \text{decade}^{-1}$ increase in stream temperatures in 25 years could result in reductions in spawner capacity of 25% for MC and 33% for TR (Table 4.5d).

Metapopulation simulations: effects of management, climate change, and dispersal

The relative effects of changes in vital rates associated with management and climate change scenarios were consistent with elasticity values, but none of the scenarios modeled were sufficient to reverse the declining population trend of the base model. Decreased egg survival resulted in a substantial decrease in λ for both LHTs, although the magnitude of the change was larger for the mixed LHT (Table 4.6). Likewise, a decrease in mean subadult survival rates had a greater positive effect on the mixed LHT compared with the migratory. An increase of 10% of the current mean survival rate for the two largest stages resulted in only small increases in the population growth rate for both LHTs, with a larger change for the migratory LHT. For both LHTs, changes to transition probabilities, or mean individual growth, had large effects on λ . In particular, an increase in the transition probability for stage 1 resulted in a larger change to λ than did an increase in subadult or adult survival rates. Increased growth in stage 1 resulted in some individuals skipping stage 2 and transitioning directly into stage 3. This accelerated growth reduced the number of time steps it took for an individual to reach reproductive size, as well as move into stages where mortality rates were lower. The positive effect of increased individual growth at this stage was large enough to counteract the negative effect on population trend of decreasing growth rates in two subadult stages (Table 4.6).

Based on our extremely conservative estimates, all scenarios we modeled suggested a high probability of the metapopulation declining below 50% of its current size in 25 years. Increased survival rates, as a result of management actions, yielded only a slight decrease in the probability of decline compared with the base model (Figure 4.8a). For the climate change scenarios, a 20% decrease in egg survival resulted in a high

probability that the population would decline by more than 90 % after 25 years, whereas climate-related changes to growth rates decreased the probability of decline (Figure 4.8b). When we modeled multiple positive changes to vital rates simultaneously, including increased growth and survival, those changes together were sufficient to counteract the negative effect of higher egg mortality and decreased subadult growth rates on the metapopulation trajectory, lowering the probability of decline (Figure 4.8c). A reduction in spawner capacity had very little effect on current population projections, because all scenarios were modeled with declining populations, which rarely met or exceeded the capacity threshold.

Changes to dispersal rates had very little effect on either the metapopulation or the individual populations under base model scenarios, in which all three populations were declining (not shown). For a scenario in which both mixed populations had growth rates close to stable ($\lambda = 0.983$) and the migratory MC population was declining precipitously ($\lambda = 0.928$), dispersal was important for maintaining individual populations. The probability that a population would fall below 75% of its current size in 25 years decreased for both MC, the population with the lowest growth rate, as well as the TR population, which started out with the lowest abundance (Figure 4.9). In contrast, the probability of decline changed very little for the largest population (SFWWR) and the metapopulation as a whole.

Discussion

Bull trout have declined in distribution and abundance across much of their native range, prompting a need to better understand how populations will react to anthropogenic stressors and climatic changes. We present a stage-structured population viability model

based on empirical vital-rate estimates, which can be used to explore the response of single and interconnected populations to changes in management, habitat availability, and habitat connectivity. The model serves as a tool with which to assess potential management actions and to better understand the role of life-history variability on population resilience.

Empirical estimates of bull trout vital rates

In this study, we compiled a complete set of vital rate estimates based on multiple long-term capture-mark-recapture studies, an uncommon undertaking for highly mobile species. Although most of our information was from a single population, we also compared population parameters among three neighboring populations, which provided important insight into variability in demographic rates and life-history strategies. We also compared our estimates to those available in the literature, where available. The relationship we established between female length and number of eggs was similar to that from other bull trout populations, including adfluvial migratory populations where fish overwinter in reservoirs or lakes (Johnston et al. 2007). Relative to other studies, our model underestimated fecundity of the largest sizes observed, so care should be taken applying this relationship to bull trout larger than 600 mm. The steep slope of the length-fecundity relationship demonstrates that larger fish produce significantly more eggs than smaller fish and helps illustrate the significant reproductive contribution that large, fluvial fish can make to populations with migratory life-history strategies.

Timing and size at maturation reflect trade-offs between survival, growth, and reproduction (Magnan et al. 2005). For bull trout, such trade-offs have likely led to the substantial amount of variation observed in demographic processes among and within

populations. In our study system, bull trout spawned at smaller sizes than has been observed in adfluvial systems (Fraley and Shepard 1989; Johnston and Post 2009). This discrepancy might simply be a characteristic of the slightly smaller body size of the fluvial life-history type compared with adfluvial fish. In the SFWWR population, the variability in size of reproductive individuals and probability of spawning at a given size describes a population that spans a life-history continuum, with mature fish found from sizes representative of resident spawners, to large sizes typical of migratory fish. A range of sizes at maturation may help stabilize population fluctuations and hedge reproductive bets, as fish that spawn earlier in their life cycle will have a higher chance of surviving to spawn, whereas fish that grow larger before spawning have a larger clutch size and therefore a higher probability of offspring survival (Crespi and Teo 2002).

Bull trout within the Walla Walla basin also displayed a wide range of growth rates that could have resulted from numerous factors, including differences in stream temperature and productivity among locations in the watershed, food availability among sites, and variability among individual fish, such as aggressive behavior. It is unclear if the observed difference in transition probabilities between the MC and SFWWR populations was due to environmental characteristics of the two stream systems, a reflection of the percentage of individuals in each population that exhibit migratory behavior, or simply an artifact of low sample sizes (Morris and Doak 2002). In addition, fish capture methods varied between the two systems; bull trout were recaptured annually throughout the SFWWR spawning patch, whereas recaptures in MC only took place at the downstream end of the patch, and thus might have preferentially sampled larger, more mobile individuals.

Faster growth rates for fishes often confer a selective advantage, as larger fish are able to escape gape-limited predators, but the potential for growth is limited by metabolic demands and available resources (Parker 1971). Because of the relationship between growth and survival, these two vital rates should ideally be estimated simultaneously (White 2000), but our low physical recapture rate did not provide sufficient data for such an analysis. Factors affecting bull trout growth in the wild remain an area of uncertainty that warrants additional research, particularly because our population models indicated that changes to individual growth rates (as indicated by higher transition probabilities) had large effects on population trend. As such, factors affecting individual growth may play an important role in the vulnerability of populations to environmental changes.

Reliable stage-specific estimates of survival are critical for stage-based population viability models to produce realistic results. We removed sampling variance from survival rate estimates, which should produce more realistic results (White 2000), but even after doing so, our estimates spanned a range of potential values. Changes to survival rates even within the range of our 95% credible intervals could have substantial effects on the outcome of population viability assessments. We considered our models to be extremely precautionary, as we estimated both λ and survival rates over a period of time during which the SFWWR population appeared to be declining.

Additionally, inclusion of stochastic processes usually provides a more realistic population projection, but may also lead to overly pessimistic extinction risk (White 2000). Our estimates of temporal variance were relatively high for the smallest stage assessed, but also for the largest stage, comprised of migratory individuals. While high variability in smaller animals is expected, the annual variability in large, migratory adults

warrants further investigation, as factors that affect survival of this life stage could relate to an interaction between their size and anthropogenic stressors that vary temporally, such as flow regulation and the ability of fish to pass barriers (Naughton et al. 2005). An understanding of the relationship between migratory adult survival and environmental covariates is particularly germane in light of the relative importance of this life stage to overall population growth for the migratory life-history type.

Elasticity patterns across life-history types

Comparison of elasticity values among bull trout life-history types provides some insights into the trade-offs between growth, survival, and reproduction that may help maintain life-history diversity within populations. The optimization approach to life-history theory suggests that organisms maximize the allocation of available resources between growth, survival, and reproduction throughout their lifetimes (Stearns 1989). The two primary bull trout life-history strategies represent different approaches to allocating lifetime resources. Migratory fish allocate more energy toward movement and growth, whereas resident fish allocate a greater portion of overall lifetime energy toward reproduction. The relative magnitude of elasticity values between the two LHTs reflects these different cost-benefit approaches. Adult survival elasticity values were higher for migratory individuals compared with other LHTs, because more of their lifetime reproductive output (and therefore contribution to future population growth) depends upon survival of mature adults. In contrast, resident LHTs have higher fertility elasticity values because more population-level resources are allocated to reproduction than survival. Our results indicate that maintenance of both life-history strategies is likely important for the persistence of bull trout populations. For example, years or

environments in which egg survival is low might confer a selective advantage for the migratory LHT, and when adult survival decreases, the resident LHT may fare better.

The elasticity patterns we observed have important implications for management and conservation of bull trout populations. First, juvenile survival appears to play an important role in population persistence regardless of life-history type. However, juvenile bull trout might reside in different parts of a watershed depending upon life-history strategy (Fraley and Shepard 1989), so knowledge of juvenile movement patterns and habitat use are important for conservation of that life stage. Second, the relative sensitivity of population growth to fertility and adult survival may vary among different populations, depending upon the proportion of individuals exhibiting a particular life-history strategy and the composition of different life stages within the population. For example, populations with a stronger migratory component could be more resilient to increased egg or juvenile mortality, but may be more affected by predation of the largest adult sizes (Hebblewhite and Merrill 2009).

Model evaluation will also be most affected by those vital rates with the highest sensitivities (Morris et al. 2002). As such, accurate estimates of juvenile survival are most important for resident populations, whereas in addition to juvenile survival, accurate estimates of adult survival are relatively more important for predictions of migratory populations. For these reasons, future management of bull trout populations can benefit from improved knowledge of representative life-history strategies, age structures, and spatial distributions.

Sensitivity analyses (including elasticity calculations) of population growth rate to changes in vital rates are common tools that provide important insights for management

aimed at changing population growth rates for conservation or control (Crouse et al. 1987; Doak et al. 1994; Aubry et al. 2010). However, elasticity analyses should be examined critically prior to prescribing conservation efforts (Wisdom et al. 2000; Koons et al. 2006). By plotting the response of population growth to changes in vital rates, were able to explore the potential for management actions that target a specific part of the life cycle to affect population trend. Prior to using elasticity values to guide management actions, this type of additional evaluation should be conducted to examine the potential for management actions to be effective (Mills et al. 1999).

A second caveat for interpreting elasticity values is that because elasticity analyses assume a stable stage distribution, sudden changes in vital rates will lead to instability in the stage structure (Crowder et al. 1994). Populations with unstable stage structures may respond differently to perturbations than elasticity predictions would suggest (Koons et al. 2006). Future analyses should evaluate the effect of sudden changes to survival rates on age structure stability, and the ensuing transient dynamics (Crowder et al. 1994; Koons et al. 2006).

Evidence of metapopulation structure and the role of connectivity

Our data provide one of the first empirical estimates of long-distance dispersal in contemporary stream conditions. Although we observed only three instances of bull trout dispersing from one population to another, these observations provide evidence that current populations in the Walla Walla basin do operate as a metapopulation. These data also support previous hypotheses that dispersal among populations occurs infrequently (Rieman and McIntyre 1995). Low rates of connectivity (historic and current dispersal combined) have been inferred from strong genetic divergence among bull trout

populations, which generally increases in relation to the distance between populations (Meeuwig et al. 2010; Ardren et al. 2011). However, dispersal rates inferred from genetic data are likely a combined metric of historic and current genetic exchange (Mills 2007). Historic levels of dispersal may have been higher than our current estimates suggest, as fish now have to contend with in-stream barriers and degraded habitat in migratory corridors. This theory is supported by evidence of an increase in genetic divergence among populations separated by anthropogenic barriers (Meeuwig et al. 2010).

Based on genetics and the small number of observations in our study, we could not detect differences in the direction of dispersal, and assumed equal dispersal in both directions in our models. Although the SFWWR bull trout population contains the largest number of marked fish within the Walla Walla basin, we did not observe a fish stray from the SFWWR into either of the other two populations, despite numerous opportunities for detection throughout the system. Although our overall sample size of marked bull trout traveling long distances is quite small, we did observe two fish migrate out of MC and into SFWWR, raising the question of whether dispersal rates are directionally asymmetric. Lower stream sections of MC are heavily modified with numerous diversions, which may result in higher stray rates for the MC population. If dispersal is more likely to occur from MC and TR into SFWWR, these populations may act as sources, even though they have fewer individuals than the SFWWR population. Therefore, the direction of dispersal is also important for understanding metapopulation dynamics.

Habitat capacity and predicted changes

In many geographic areas, an important first step in bull trout conservation planning is simply to identify the quality and distribution of available habitat. The rule set we used to estimate bull trout spawning habitat produced reliable results in the Walla Walla basin, and was based on data readily available for the entire Columbia River basin and implemented with GIS software. Further development of this approach could help researchers identify habitat variables that consistently predict bull trout spawning habitat in other similar stream systems (e.g., Bartz et al. 2006). Elevation, stream temperature, and gradient were important predictors of spawning habitat in the Walla Walla basin, and have also been associated with bull trout occurrence in other systems (McCleary and Hassan 2008; Wenger et al. 2011). This consistency among studies suggests that bull trout spawning habitat can be predicted based on physical habitat variables at the stream reach scale from GIS data, which is useful in many places where distribution data are unavailable.

Our estimates of spawning habitat loss due to stream temperature warming varied considerably among spawning patches. The greatest predicted loss of habitat occurred in the TR because the majority of current spawning habitat was located at slightly lower elevations than the other populations, and habitat was distributed in numerous tributaries near the initial isotherm boundary. By comparison, we predicted considerably less habitat loss in the SFWWR because all spawning tributaries were more than 10 km above the isotherm boundary, and there was no tributary habitat lost. Our predictions of potential habitat loss were substantial, but they were based on the assumption that the distribution of bull trout spawning habitat is currently limited by temperature. Numerous

other factors also affect spawning distributions, including spawning gravel distribution and groundwater influence, the latter of which could help mitigate stream warming rates (Boulton et al. 1998). Further, like many stream fishes, bull trout may exhibit more behavioral plasticity than habitat models alone would predict (Howell et al. 2010). Estimates of habitat loss associated with stream temperature demonstrate one potential effect of climatic change, and illustrate that the consequences of stream temperature warming could vary considerably among populations depending upon the spatial arrangement of available habitat and the quality of habitat near a temperature boundary.

Metapopulation responses to management and climate change

The current study demonstrates the utility of evaluating a range of potential changes in demographic rates across multiple population types to help evaluate conservation and management actions. Given the inherent uncertainty in parameter estimates and baseline population information, such as initial abundance, population simulations preclude absolute predictions of extinction probabilities or future population sizes. Nonetheless, comparison of responses to changes in survival, reproductive, and growth rates provide valuable insights into potential population responses. Overall, our scenarios demonstrate that small changes to vital rates were insufficient to reverse a population in relatively steep decline, such as we modeled. As such, management actions aimed at reversing a dramatically declining trend would need to have larger effects, or would need to target a positive response from multiple vital rates and multiple life stages, rather than focus on a single portion of the life cycle. Additionally, because the response of a population to such changes will vary depending upon the life-history characteristics of its individuals, metapopulations with different numbers of subpopulations and a

different combination of life-history types could respond differently to the same perturbation scenarios we described here. Thus, knowledge of population stage structure and life-history traits are important for management decisions, even at the metapopulation scale.

Our metapopulation projections demonstrated three examples of potential effects of climate change on demographic rates of a migratory freshwater fish, each of which had a very different influence on metapopulation dynamics. Decreases in survival at any life stage resulting from stream temperature warming would clearly be detrimental to population persistence. However, the potential positive effects of changes to the metabolic rates of organisms has garnered much less attention (Doak and Morris 2010). In our simulations, the relative magnitude of the positive population response to increased individual growth rates was sufficient to counteract the combined negative effects of changes to other vital rates. Similar types of compensatory changes in demographic rates have been observed in other species, effectively buffering populations against the negative effects of climate change (Doak and Morris 2010). However, such compensatory mechanisms are unlikely to persist as streams continue to warm. Continued warming can be expected to result in the deterioration of one or more vital rates past the point of compensation, resulting in a rapid population decline once this "tipping point" has been passed (Doak and Morris 2010).

For a stenothermic fish like bull trout, increases in stream temperature above an optimal threshold can lead to a number of other potentially negative biological responses, including reduced fitness via susceptibility to disease, increased metabolic costs, or changes in spawn timing (Crozier et al. 2008; Warren et al. 2012). Our results suggest

that the response of bull trout populations to climate change might be difficult to identify or predict, as the effect on individual vital rates could be synergistic or confounding (Crozier et al. 2008). As such, long-term monitoring of representative populations, such as those used in this study, will be important to detect demographic compensation and identify tipping points beyond which compensation can no longer occur (Doak and Morris 2010).

The limited response of metapopulation persistence to decreased carrying capacity was unsurprising, given the declining population growth rates used in our simulations (Ginzburg et al. 1990). Under the scenarios we examined, populations only rarely reached carrying capacity in stochastic simulations. We expect that changes to carrying capacity could have very different effects on populations experiencing positive growth rates, or if a different type of density-dependence function were included in the population model (Ginzburg et al. 1990). Additionally, we based our estimates of reduced capacity on the portion of habitat lost from spawning survey index reaches, which represented only a portion of total habitat lost. Thus, to detect effects of gradually increasing stream temperatures on the distribution of organisms, monitoring should take place throughout the entire habitat of concern.

Results of our metapopulation model indicate that under the scenarios we examined, the importance of dispersal differed for individual populations depending upon the combined dynamics of those populations, whereas the metapopulation response was relatively insensitive. For a metapopulation in which some populations are stable within a stochastic setting, dispersal can help decrease the extinction risk for small and declining populations (Hanski and Simberloff 1997). Although dispersal rates at the upper end of

what we evaluated are may not be realistic for bull trout, this effect was apparent even at dispersal rates of less than 2% of the reproductive adult population.

According to metapopulation theory, the low rates of dispersal we observed indicate that the populations of bull trout in the Walla Walla basin could be described as somewhere between a Levins and a non-equilibrium type of metapopulation. In a classical Levins model, a metapopulation is comprised of multiple small subpopulations, and dispersal is sufficient to recolonize extinct or empty patches. In a non-equilibrium metapopulation, subpopulations are separated by large distances and each is extinction-prone because of its isolation and relatively small size (Harrison and Taylor 1997). As ours are some of the first empirical estimates of bull trout dispersal, we have no way of assessing historic or potential levels of movement between populations to evaluate how this metapopulation type may have changed over time. Given our current dispersal estimates, recolonization of extinct or unoccupied patches is unlikely to occur. However, even low rates of dispersal can help stabilize smaller populations, and the exchange of even one or two individuals per generation could be sufficient to help maintain genetic diversity and prevent genetic bottlenecks (Mills and Allendorf 1996).

Implications for bull trout conservation

This research provides a nearly comprehensive set of vital rate estimates for seven size classes of bull trout based on robust empirical estimates from multiple, long-term datasets. These estimates help establish important baseline parameters that can be used to evaluate population-level responses to management actions or environmental changes (e.g., Crowder et al. 1994). The general patterns described by our sensitivity analyses and population projections can help managers develop broad-scale conservation priorities

based on life-history strategies (Heppell et al. 2000). We expect bull trout populations to have the greatest response to changes in juvenile survival rates, as well as to individual growth rates. Accordingly, bull trout populations may be particularly susceptible to environmental changes that affect bioenergetics, including stream productivity, food availability, and temperature. Our findings also indicate that resident populations are more responsive to changes in fertility rates and vital rates of early life stages, whereas migratory populations are more sensitive to loss of large, fecund adults, in addition to juvenile survival and growth rates. Further, results of our modeling indicate that to reverse steep population declines, management actions should target improvement of multiple life stages simultaneously.

In a metapopulation context, recolonization of extinct patches may be unlikely under low rates of bull trout dispersal, particularly when patches are separated by large distances (Harrison and Taylor 1997). As such, individual populations warrant unique consideration with regard to conservation actions. However, maintenance of connectivity to facilitate dispersal is still important to promote genetic exchange among populations and to allow the potential for populations to help equalize one another during asynchronous catastrophic events.

Diversity in life-history strategies, migratory patterns, and behavioral plasticity within populations likely helps spread the risk of environmental stochasticity, both spatially as bull trout occupy a range of habitats, and temporally, via numerous co-existing generations that reproduce at different sizes (Rieman and McIntyre 1993). Our findings indicate that this diversity enhances demographic stability and is therefore important for long-term population persistence (Gross 1991). Because vital-rate

perturbations affect population growth rates differently among life-history types, the severity of anthropogenic stressors or environmental changes might vary widely among bull trout populations, depending upon the composition of life-history strategies within the population. Variation in demographic responses can help stabilize population growth rates for populations in which vital rates differ considerably among individuals in the same population, such as in the SFWWR. The same could be true for metapopulations composed of populations with different proportions of life-history types (Stacey et al. 1997). To provide as much demographic stability as possible, diversity within and among populations should be maintained along a continuum that emphasizes conservation of the full range of life-history traits expressed by bull trout.

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Table 4.1. Stage-specific total lengths (TL) and demographic parameters estimated from two bull trout populations. Survival rates, temporal variance (SD), and spawning probability were estimated from the South Fork Walla Walla River, Oregon (SFWWR). Transition rates (probability of growing from one stage to the next in one year) were estimated based on recapture data from the SFWWR and Mill Creek (MC) populations. For simplicity, low transition rates (<0.01 were omitted) and transition rates that spanned multiple stages were combined (see supplementary material Table B2).

Stage	TL (mm)	Survival	SD	Spawning probability	Transition probability (SFWWR/MC)
1	60 to 120	0.218	0.205 ^a	NA	1.00/ND
2	120 to 180	0.264	0.205	ND	1.00/0.54*
3	180 to 240	0.382	0.097	0.05	0.88/0.83
4	240 to 300	0.384	0.165	0.10	0.70/ND
5	300 to 360	0.389	0.048	0.30	0.33*/0.83
6	360 to 420	0.444	0.076	0.33	0.20/0.76
7+	>420	0.471	0.189	0.70	NA

ND indicates no data

NA indicates a parameter that was not applicable to a particular life stage

^aSD for stage-1 was assumed from stage-2 estimates

*indicates low sample size

Table 4.2. Lower-level vital rates included in population models for migratory, mixed, and resident bull trout life-history types. A parameter that was not applicable to a particular life stage is indicated by NA.

Parameter	Migratory	Mixed	Resident
m_2	NA	227	227
m_3	NA	450	450
m_4	NA	750	641
m_5	1128	1128	1059
m_6	1583	1583	NA
m_7	3184	2623	NA
B_2	NA	0.025	0.100
B_3	NA	0.100	0.330
B_4	NA	0.180	0.600
B_5	0.300	0.500	0.900
B_6	0.400	0.400	NA
B_7	0.900	0.900	NA
S_{egg}	0.43	0.43	0.43
S_0	0.284	0.284	0.284
S_1	0.218	0.218	0.284
S_2	0.264	0.264	0.218
S_3	0.384	0.384	0.264
S_4	0.389	0.389	0.389
S_5	0.444	0.444	NA
S_6	0.471	0.471	NA
γ_1	1.000	1.000	1.000
γ_2	1.000	0.800	0.180
γ_3	1.000	0.740	0.340
γ_4	0.850	0.600	0.200
γ_5	0.830	0.500	0.120
γ_6	0.750	0.700	NA

m_i = number of eggs per stage median total length

B_i = proportion of females attempting spawning

S_i = probability of survival for an individual in stage i

γ_i = probability of growing from stage i into $i + 1$

Table 4.3. Metrics used to assess population connectivity within the Walla Walla basin: (a) dispersal rates between populations based on the proportion of marked fish observed moving from one population to another, (b) dispersal rates estimated from a movement function developed from combined capture-mark-recapture movement data, and (c) migrants per generation based on genetic divergence between populations (pairwise F_{st} values). For (a) estimates describe rates of dispersers moving from each population in a column into the populations in rows, (b) dispersal is based on distance, so assumed equal in either direction, and (c) indication of genetic exchange assumed equal in either direction.

	(a) Recapture dispersal rate per 7 years			(b) Dispersal function rate (applied annually in model)			(c) Migrants per generation (i.e. dispersers per 7 years)		
	SFWWR	MC	TR	SFWWR	MC	TR	SFWWR	MC	TR
SFWWR		0.0052	0.0000						
MC	0.000		0.0098	0.002			3.580		
TR	0.000	0.000		0.0014	0.0015		3.440	2.380	

Table 4.4. Rule set used to define four categories of spawning habitat in the Walla Walla basin, Oregon. All spawning density data was based on bull trout redd censuses in the Walla Walla basin during the Columbia Plateau's bull trout Ecological Monitoring and Assessment Program assessment (EMAP); physical habitat attributes were downloaded from the Ecosystem Diagnosis and Treatment (EDT) analysis (Mobernd Biometrics 2004).

Habitat type	Rule set	Mean stream width (m)	Maximum density (redds·km ⁻¹)
No spawning	<700 m elevation Or gradient <0.01725 and >0.0745 Or max mean monthly temp >1.95 (rating)	NA	0
Low density spawning	Gradient <0.027 and >0.01725 And max mean monthly temp <1.95 and >1	13	6
High density spawning	Gradient ≥0.027 and <0.0745 And min (low flow) width >4.5 m	9	64
Spawning tributary	Gradient >0.04 and <0.0745 And min (low flow) width <4.5 m and >0 m	1.5	19

Table 4.5. Isotherm shift rates (ISR), bull trout habitat, and spawner capacity estimated for current and future conditions in the Walla Walla basin. Future estimates are predicted for 2035 based on four rates of stream warming. (a) Isotherm shift rates (the rate at which a stream temperature threshold is expected to shift upstream, shown for a range of channel slopes. Spawning habitat predicted from the spawning capacity rule set for (b) entire spawning patches and (c) spawning survey index reaches only. (d) Maximum number of redds based on spawning habitat in redd survey index reaches.

(a) Isotherm shift rate ($\text{km} \cdot \text{decade}^{-1}$)

% Channel slope	Stream warming rate ($^{\circ}\text{C} \cdot \text{decade}^{-1}$)			
	0.1	0.15	0.2	0.3
0.5	4.2	6.3	8.3	12.5
1	2.1	3.1	4.2	6.3
2	1	1.6	2.1	3.1
3	0.7	1	1.4	2.1
5	0.42	0.63	0.83	1.25

(b) Spawning habitat (km) predicted from capacity function

Population	Current	In 2035 with stream warming rate ($^{\circ}\text{C} \cdot \text{decade}^{-1}$)			
		0.1	0.15	0.2	0.3
SFWWR	45.1	40.7	38.5	36.4	32.0
MC	21.8	17.9	16.0	13.6	11.7
TR	43.7	34.2	29.4	21.1	10.5

(c) Spawning habitat (km) in redd survey index reaches

Population	Current	In 2035 with stream warming rate ($^{\circ}\text{C} \cdot \text{decade}^{-1}$)			
		0.1	0.15	0.2	0.3
SFWWR	11.9	11.9	11.9	11.9	11.9
MC	17.6	14.7	12.9	11.5	10.1
TR	22.0	17.6	15.5	9.9	6.1

(d) Estimated spawner capacity in index reaches (max. # redds)

Population	Current	In 2035 with stream warming rate ($^{\circ}\text{C} \cdot \text{decade}^{-1}$)			
		0.1	0.15	0.2	0.3
SFWWR	478	478	478	478	478
MC	395	383	370	337	288
TR	690	612	573	396	245

Table 4.6. Population growth rate (λ) for each life-history type based on changes to parameters in our base model, where $\lambda = 0.931$ ($\lambda < 1$ indicates a declining population growth rate). Hypothetical mechanisms for changes in individual demographic parameters related to Management (M), climate (C), or both (CM) are shown.

Scenario	Hypothesized mechanism	Change in parameter	Migratory λ	Mixed λ
C 1	Increased winter scour and redd sedimentation due to higher winter flows	Decrease S_{egg} by 20%	0.903	0.893
M 2	Improved habitat in rearing areas due to management actions	Increase S_2 and S_3 by 10%	0.950	0.962
M 3	Improved passage through migratory corridor	Increase S for two largest stages by 10%	0.948	0.939
C 4	Higher growth rates due to increased water temperatures in spawning areas	Increase stage 1 growth rate by 10%	0.962	0.979
C 5	Lower growth rates for subadult stages resulting from increased water temperatures (above optimum)	Decrease stage 3 and 4 growth rate by 10%	0.922	0.913
C 6	Elevated water temperatures throughout the system	C4 and C5 combined	0.943	0.969
C 7	Elevated water temperatures throughout and increased winter flows	C1, C4, and C5 combined	0.928	0.947
CM 8	Elevated water temperatures, increased winter flows, improved passage	C1, C4, C5, and M3 combined	0.945	0.955
CM 9	Elevated water temperatures, increased winter flows, improved passage, and improved rearing habitat	C1, C4, C5, M2, and M3 combined	0.968	0.983

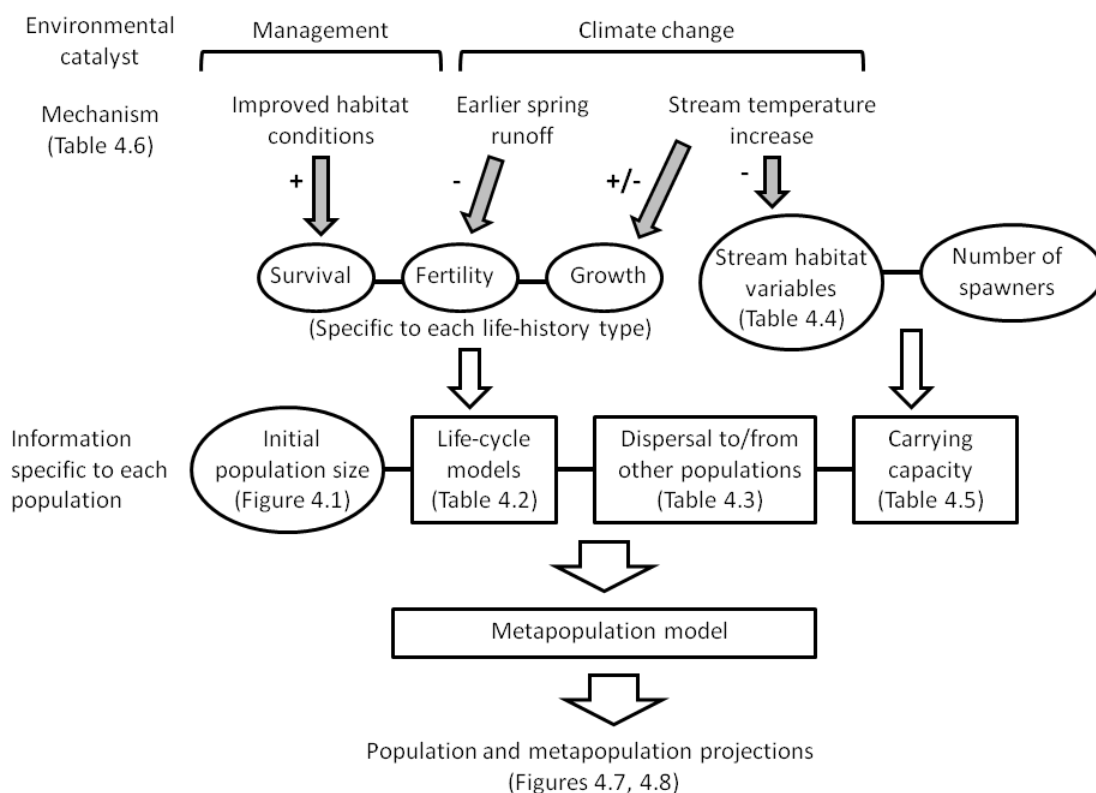


Figure 4.1. Schematic representation of components used in metapopulation model projections, with associated references to tables and figures where applicable. Model parameters that were based on empirical measurements are depicted with an oval, and components that describe a model are outlined with a rectangle. Model inputs are shown by an open arrow. Changes to model inputs based on hypothetical management and climate changes are shown with a gray arrow, and an increase (+) or decrease (-) in the response is shown next to the arrow.

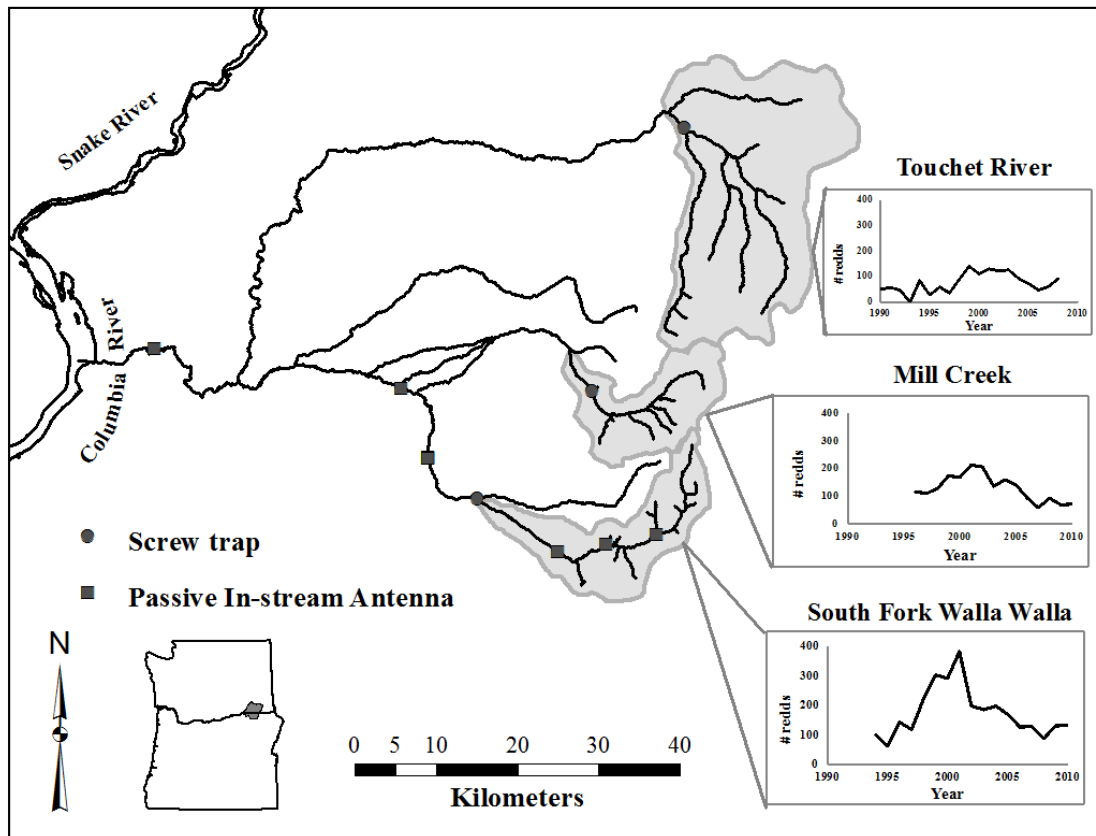


Figure 4.2. Three bull trout populations located within the Walla Walla River basin, Oregon and Washington: Touchet River, Mill Creek, and South Fork Walla Walla River. Watershed outlines depict spawning habitat patches, where spawning and juvenile rearing occurs, and bull trout migrate throughout the basin. Graphs show the number of redds counted in index reaches for each of the three populations from 1990 through 2010.

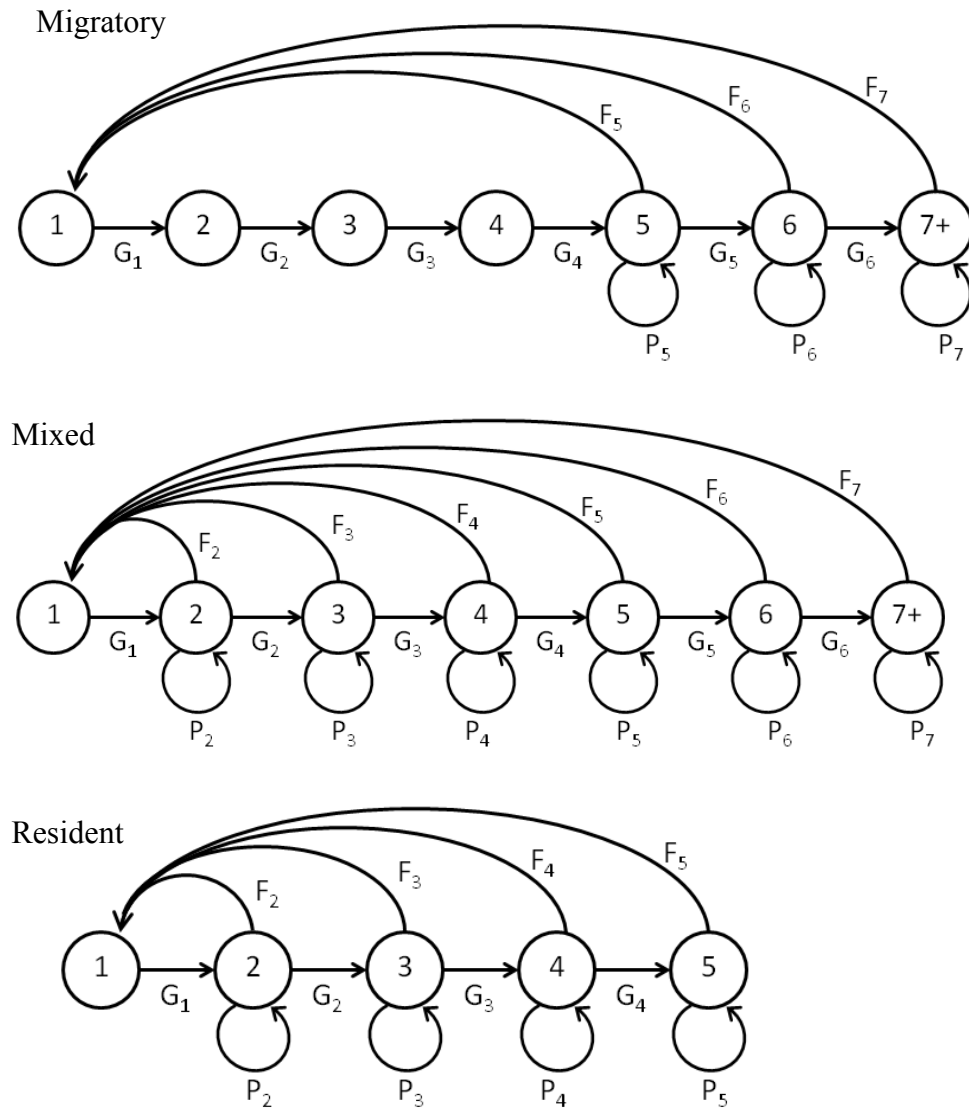


Figure 4.3. Life cycle diagrams describing migratory, mixed, and resident bull trout life-history types. G_i represents the probability of surviving in stage i and growing into the next stage, P_i is the probability of surviving and staying in the same stage, and F_i represents the fertility contribution of each stage, the total number of female eggs expected to live to stage 1. Life cycle element estimates are shown in Tables 4.1 and 4.2.

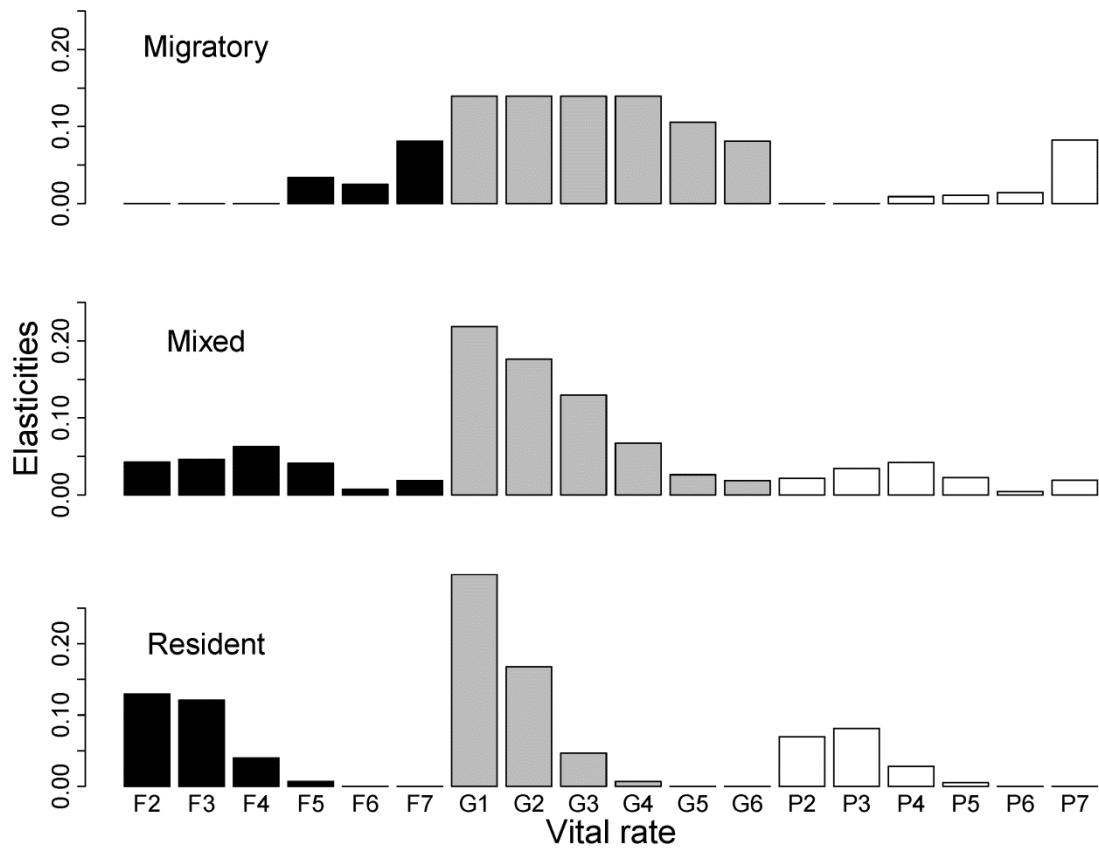


Figure 4.4. Elasticity values of stage-specific matrix elements for three different bull trout life-history types. Black bars represent elasticity values for fertility rates, gray bars represent elasticities associated with the probability that an individual survives and grows into the next stage, and open bars represent elasticities for the probability that an individual survives and remains in the current stage.

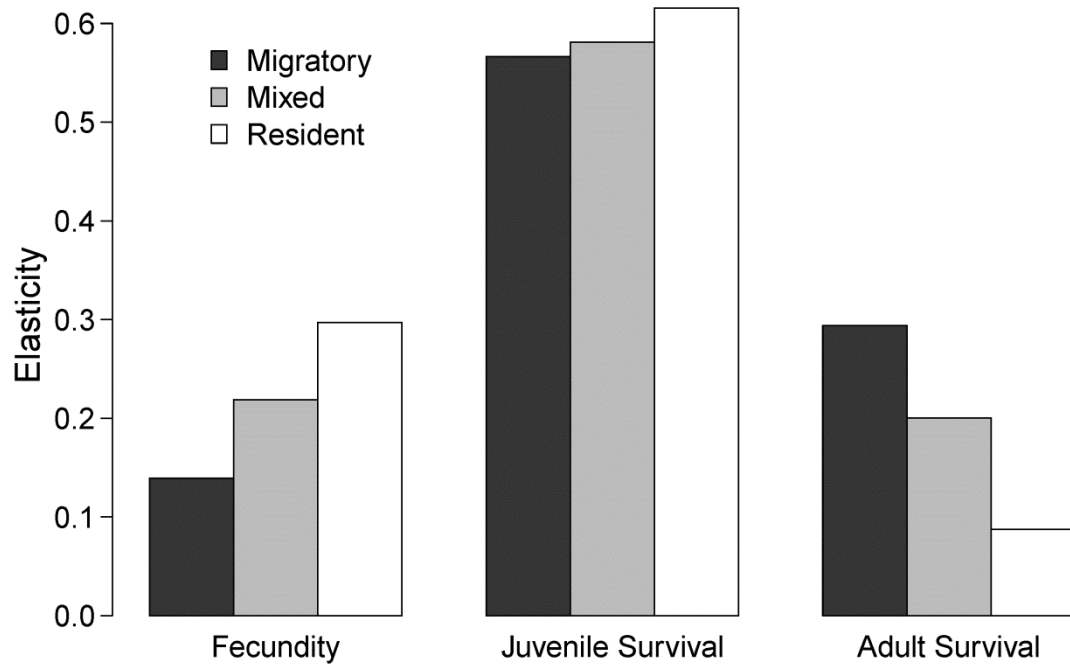


Figure 4.5. Elasticity values representing matrix elements for fertility, juvenile survival, and adult survival combined across life stages for three different bull trout life-history types. Elasticities for fertility are summed across all stages; juvenile survival represents the sum of G_1 through G_4 and P_2 through P_4 for migratory and mixed life-history types, and $G_1 + G_2 + P_2$ for the resident type; adult survival is the sum of all remaining matrix elements.

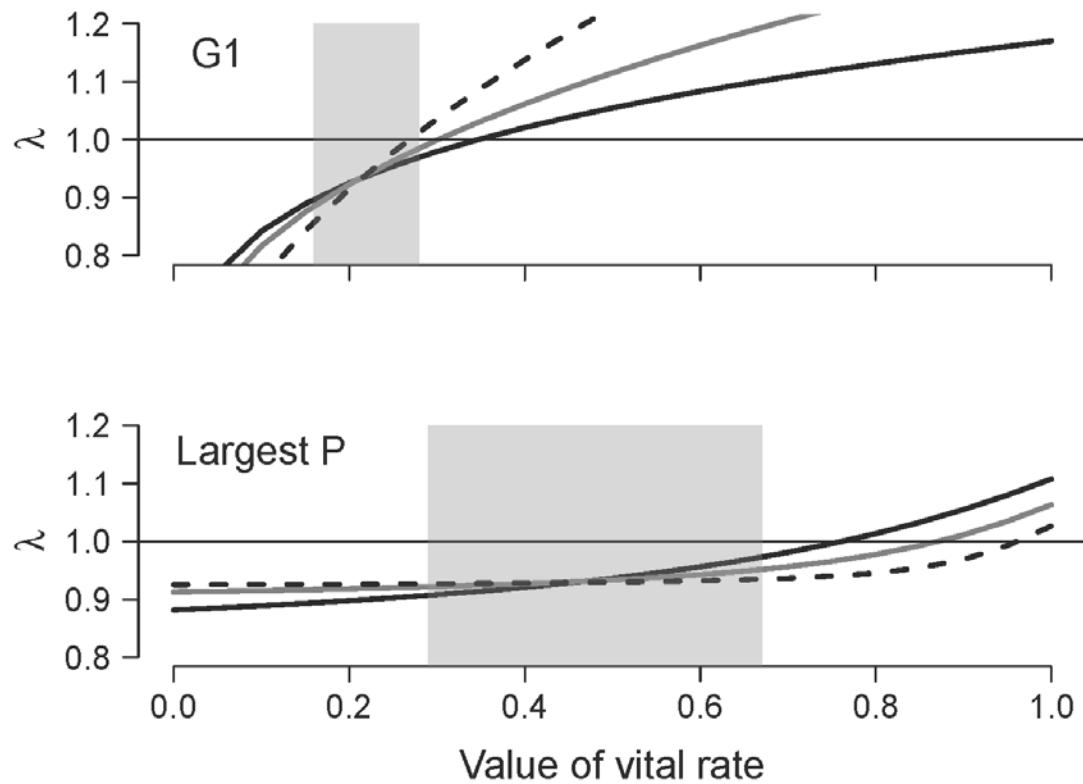


Figure 4.6. Response of population growth rate (λ) to changes in a single matrix element across a range of values while holding all other elements constant for the migratory (solid black line), mixed (gray line), and resident (dashed line) life-history types. Matrix elements are described in Figure 2; the largest value of P refers to P_7 for the migratory and mixed life-history types, and P_5 for the resident type. A horizontal reference line shows a reference value of $\lambda = 1$, and shaded areas represent the range of possible values for each vital rate based on 95% confidence intervals (for G1) or 95% credible intervals (for P).

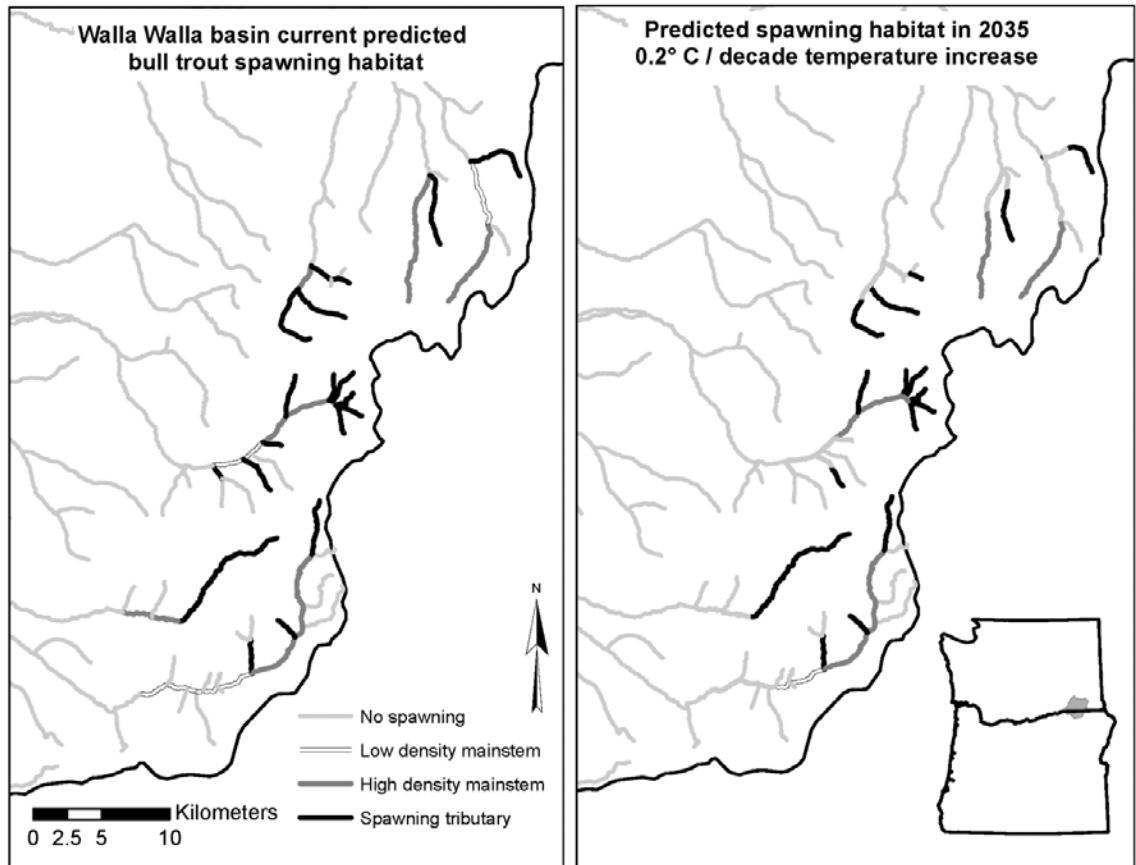


Figure 4.7. Three categories of suitable spawning habitat in the Walla Walla basin under current conditions (left panel), and predicted available spawning habitat in 25 years (2037) based on a 0.2 °C per decade increase in stream temperatures (right panel). Spawning habitat types were based on the rule set described in Table 5.

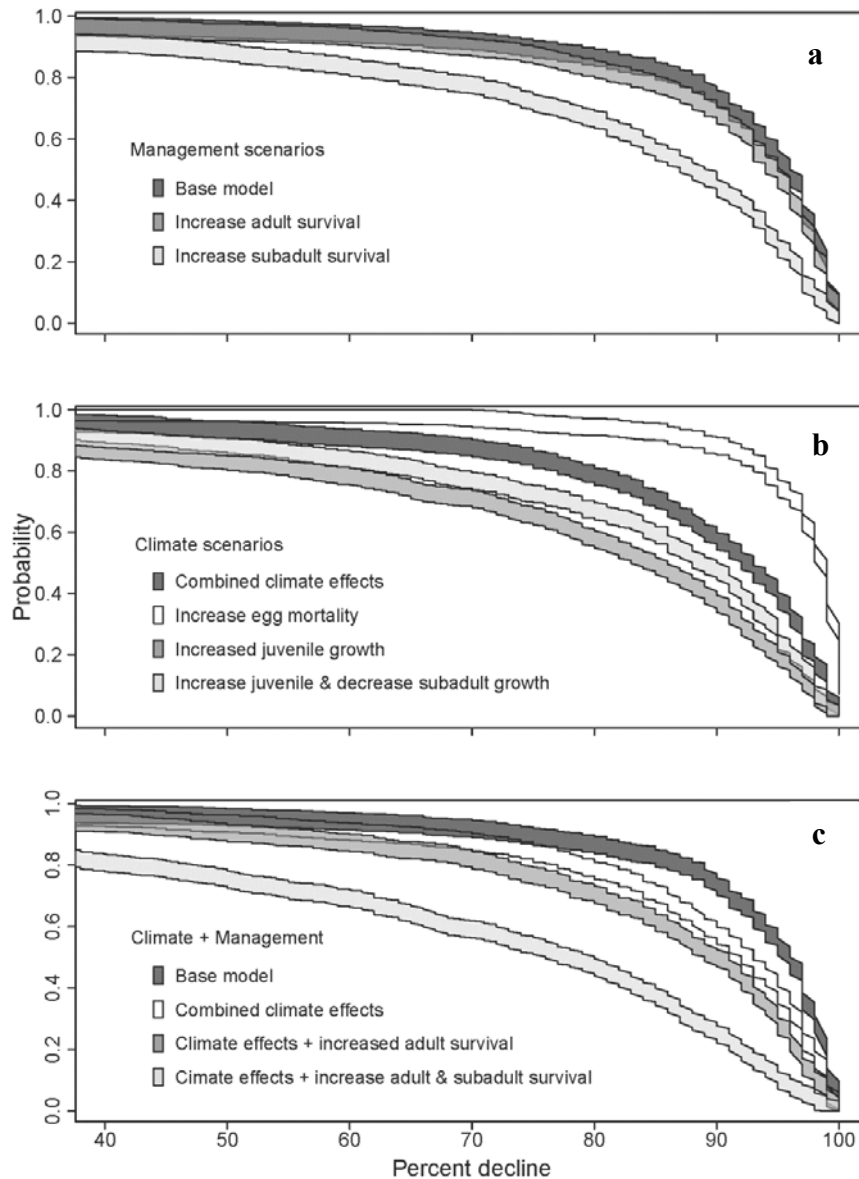


Figure 4.8. Effects of potential changes to vital rates resulting from changes in climate or management on the probability of the Walla Walla basin metapopulation declining by a percentage of the current population size in 25 years, assuming a baseline population growth rate of $\lambda=0.931$. The width of the band represents 95% confidence intervals.

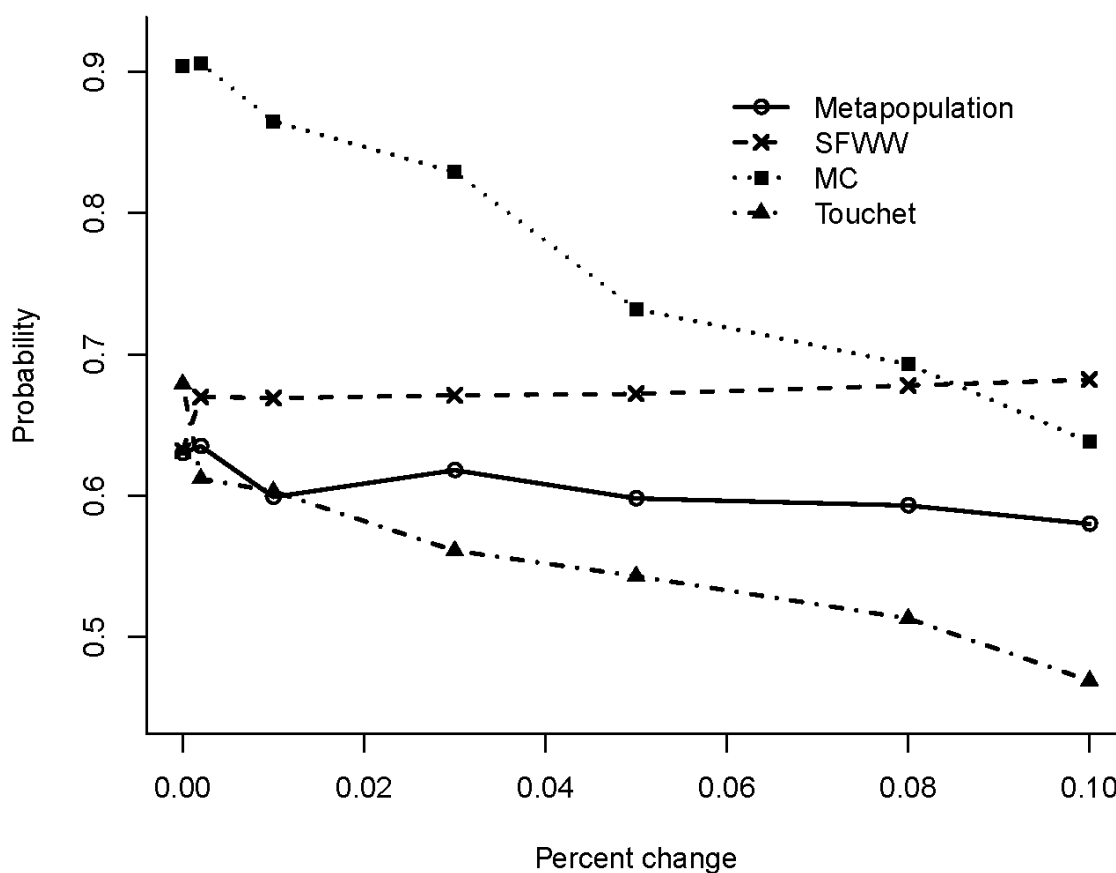


Figure 4.9. Effects of varying dispersal rates on the probability that a population will fall below 75% of its current population size in 25 years based on a scenario in which all three sub-populations were affected by climate-related changes in vital rates, and positive management actions were applied to the SFWWR and TR populations ($\lambda = 0.983$), but not to the MC population ($\lambda = 0.928$).

CHAPTER 5

SUMMARY AND CONCLUSION

Patterns of movement, habitat use, and life-history diversity of stream fishes reflect the evolutionary pressures of the physical environment. The variation in maturation, migratory behavior, and life-history strategies exhibited by bull trout likely help to stabilize populations in variable stream environments (Rieman and McIntyre 1993). Coexisting life-history forms within a single population can help disperse risks associated with environmental stochasticity, as individuals occupy a variety of habitats throughout the riverscape (Groot and Margolis 1991). One life-history type might dominate under a certain set of conditions, while another may be favored when a different range of conditions prevail (Gross 1991). Spatial and genetic diversity among populations can also provide stability, as multiple populations are unlikely to experience a catastrophic event all at the same time (Hanski and Gilpin 1991). However, for many imperiled populations, these life-history adaptations are insufficient to contend with the rapid pace and geographic extent of anthropogenic changes (Brook et al. 2000). As bull trout face different threats to individual components of their life cycle across multiple spatial and temporal scales, a multi-scale perspective is imperative for effective conservation and management.

In my dissertation research, I examined factors affecting demographic rates of bull trout populations at spatial scales ranging from individual redds to a metapopulation composed of three distinct populations whose natal spawning patches were between 70 and 120 km apart. I focused on components of the bull trout life cycle which have not been well documented: early life-history survival and juvenile migration, rates of

dispersal among distinct populations, and metapopulation structure. From this research, it is clear that bull trout require access to the entire riverscape to express their diverse life cycles and maintain population viability.

Bull trout spawning occurs in headwater streams where, in many locations around the West, habitat is relatively pristine and therefore the potential for management or restoration is limited. In some headwater systems, however, forest practices, livestock grazing, and road building can add sediment to spawning areas, degrade riparian habitat, and alter hyporheic flow patterns through separation of the stream channel from the floodplain and loss of channel complexity (Baxter et al. 1999; Hester and Gooseff 2010). My research on bull trout incubation success in three distinct stream systems indicates that egg-to-fry survival is negatively related to the percent of fine sediment in redds and positively related to hydraulic conductivity, the capacity for water to flow through gravel interstices. These results provide additional support for the importance of limiting anthropogenic sources of fine sediment in spawning habitat. I also observed that embryo survival was positively related to the strength of downwelling within redds, suggesting that areas with strong downwelling potentially help mitigate the negative effect of fine sediments. As such, management actions that preserve and restore stream habitat complexity likely benefit egg and larval survival by creating areas with localized downwelling above log jams and bedforms such as the transition between a pool and riffle (Tonina and Buffington 2009).

Restoration and protection of spawning habitat will also benefit juvenile bull trout rearing in the same environment, as small bull trout use complex habitat for cover and take refuge in gravel interstices (Goetz 1997). I provide some of the first empirical

estimates of survival for juvenile (ages-1 and -2) bull trout in a relatively pristine, headwater tributary. These estimates provide important baseline information for evaluating the effect of management actions and potential environmental changes on juvenile life stages. Juvenile bull trout emigrated continually from natal habitat, and thereby significantly biased survival estimates unless emigration was directly incorporated into analyses. Juvenile movement patterns occurred across a temporal and spatial continuum, with downstream movements ranging from 1 to 50 km. Juvenile bull trout migrated over the entire year, including during the winter, when adult bull trout are typically considered sedentary (Bahr and Shrimpton 2004). There did not appear to be a clear temporal or size cue for juvenile emigration from natal habitat. Movement patterns could be related to fish density in spawning habitat, stream productivity, or individual fish growth or metabolic rate (Jonsson and Jonsson 1993). Clearly, studies conducted at the stream reach scale would not be able to detect the range of movement or the diversity in patterns exhibited by juvenile bull trout. Overall, the results from this component of my research indicate that restoration of stream habitat and decisions regarding passage and flow management should consider the diverse behavior of juvenile bull trout and the range of habitat they use throughout the year.

I integrated research from a single river system with studies from neighboring rivers within the same basin to evaluate the demographic implications of different populations of bull trout within multiple rivers interacting as a metapopulation. I combined estimates of embryo survival from Chapter 2 and juvenile survival from Chapter 3 with empirical estimates of life- stage-specific growth, survival, and fecundity rates to create a demographic model for bull trout. I structured this model to describe two

different bull trout life-history types: 1) a migratory life-history type that grows quickly, reaches maturity at 300 mm total length (TL), and contains large adults (>500mm TL), and 2) a resident life-history type that grows slowly, reaches sexual maturity between 150 to 200 mm TL, and reaches maximum size around 300 mm TL. I also described another type of bull trout population that contained both migratory and resident individuals (a “mixed” life-history type), and which exhibited a combination of the traits described for the two life-history strategies. Based on intensive monitoring of a population in the South Fork Walla Walla River, bull trout appear to exhibit a continuum of migratory and growth behavior, probably best described by a mixed life-history type model. Other bull trout populations might also exhibit a range of life-history characteristics, but sampling techniques are not always established to evaluate such variability.

When I evaluated the sensitivity of overall population growth rate to changes in specific vital rates, I found that for all life-history types, juvenile survival had the greatest impact on population growth rate. This result is consistent with other organisms with relatively low survival rates, high fecundity, and no parental care (Heppell et al. 2000). This observation serves as an important reminder that small changes to juvenile survival rates can have large impacts on overall population growth rate, and further emphasizes the importance of management actions that consider juvenile habitat needs and barriers to juvenile passage throughout a river system.

When comparing among life-history types, population growth rates were most sensitive to changes in survival and fertility rates of large adults for the migratory life-history type. In contrast, the opposite was true for the resident type, which showed greater sensitivity to changes in fertility and survival of small adults. These insights into

the relative vulnerabilities of populations suggest that population structure can play an important role in the resiliency of a population to various environmental changes. To maintain populations composed of mostly resident individuals, conservation actions focused on headwater habitats will be most effective, and any loss of spawning habitat or decline in early life-stage survival will have dramatic effects on population growth and persistence. Management actions that protect the largest, oldest individuals will likely play an important role in maintaining populations with significant migratory components. As such, knowledge of current population structure will best guide effective management decisions.

In addition to providing important diversity within bull trout populations, the range of movement distances displayed by bull trout also link populations to one another. I documented dispersal of marked fish among three populations within a watershed, demonstrating that bull trout populations effectively operate as a metapopulation with limited dispersal. I simulated the metapopulation 25 years into the future based on current demographic rates, and evaluated the effect of different levels of dispersal. I found that under current conditions, with all three populations assumed to be in decline, dispersal rates had little effect on overall the probability of persistence for the metapopulation or individual sub-populations. However, under conditions where one population was declining while the other two were stable, dispersal was important to help equalize the size of individual populations, effectively lowering the probability of decline for small or declining populations.

I also evaluated potential future demographic responses to management and climatic changes. Demographic models indicated that changes in individual growth rates

had a notable influence on population dynamics, particularly during juvenile life stages. Stream temperature warming associated with climate change could result in either increased bull trout growth rates, and/or decreased growth and/or survival rates (Crozier et al. 2008). Thus, it is difficult to predict how populations will respond to a changing climate. I observed that relatively minor increases in individual growth rates could result in substantial increases in overall population trend, and could potentially compensate for decreases in other demographic rates. This type of demographic compensation could help buffer populations from the effect of climate change in the short term. However, as the climate continues to warm, eventually a portion of the life cycle will be pushed past its ecological tipping point (Doak and Morris 2010), leading to population decline or extinction, unless populations can adapt concurrently.

My dissertation research indicates that the diversity of life-history strategies expressed by bull trout help maintain demographic stability within and among populations. In the face of increasing anthropogenic threats and climate change, maintaining life-history diversity will be even more imperative for conservation and recovery of bull trout populations. Habitat heterogeneity and behavioral and life-history diversity are important for maintaining the full range of ecological and evolutionary function for bull trout populations. While logistical constraints often force managers to focus on small sections of a watershed, or a single aspect of a species' life cycle, effective long-term conservation plans should be considered at a scale that reflects the complete scope of a species' life history. Already, many bull trout populations have become more homogenized, often through the loss of the migratory life-history strategy (Nelson et al. 2002). This homogenization, coupled with habitat loss, will reduce the capacity for

diversity, and therefore resiliency to additional anthropogenic and climatic stressors. For bull trout, long-term conservation of individual populations and interacting metapopulations requires maintenance of a range of available habitat throughout a river system. For bull trout to express their full range of life-history diversity, they require adequate habitat from headwater spawning areas, to mid-watershed migratory corridors and feeding areas, to connectivity with larger river habitats that allow bull trout to disperse among populations.

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APPENDICES

Appendix A **Table A.1.** Average bull trout redd characteristics based on studies in the United States and Canada. Data is summarized in McCollister 1994 from Goetz 1989 unless marked with an asterisk. When the smallest size class of fine sediment was <6 mm, data straddle the columns for the two smallest size classes.

Reference	Stream	Surface area (m ²)	Pocket depth (m)	Fines <4 mm (%)	Gravel 4 to 6.3 mm (%)	Gravel 6.4 to 63 mm (%)	Cobble >64 mm (%)	Velocity (m·s ⁻¹)	Egg depth (m)
McCollister 1994	Jack Ck., OR	1.67	0.34	18		69	13	0.4	NA
Shepard 1984	Flathead R., MT	2.3	0.28	13	39	30	18	0.29	0.15
Allen 1980	Clearwater R., AB	0.69	0.24	10	72	12	5	0.52	0.15
Allen 1980	Timber Ck., AB	0.62	0.58	9	70	14	4	0.44	0.13
McPhail and Murray 1979	MacKenzie Ck., BC	0.5	NA	8	61	31	0	0.6	0.2
Oliver 1979	Wigwam R., BC	1.47	0.34	30		50	20	0.43	0.15
Leggett 1980	Kootenay R., BC	0.73	0.77	12		59	29	0.33	0.11
Hunter 1973	Various rivers, WA	3.59	1.05	30		60	10	1.71	NA
Blackett 1968	Hood Bay, AK	0.6	0.4	30	32	28	10	0.75	0.15
Weeber 2007*	Metolius R. tribs., OR	1.96	0.29	1	3	85	11	0.47	0.21
This study*	Metolius R. tribs., OR	1.12	0.54	6	13	72	9	0.33	NA

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APPENDIX B

BULL TROUT GROWTH, SPAWNING MIGRATIONS,
FECUNDITY, AND SURVIVAL

Between 2002 and 2012, we sacrificed a total of 62 bull trout from the South Fork Walla Walla River (SFWWR), Oregon. We removed sagittal otoliths to estimate age, and used this data to develop a von Bertalanffy growth model to estimate age-at-length (Iseley and Grabowski 2007). Based on available data, the von Bertalanffy equation for the SFWWR bull trout population was

$$L_t = 1134(1 - e^{-0.07(t+0.02)}),$$

where L_t is the length of the fish at time (or age) t (Figure B.1). We used this model, combined with growth estimates from mark-recapture data, to establish stages for bull trout that represented age classes (Table B.1).

We counted eggs from 22 sacrificed mature females and used non-linear regression to develop a fecundity-to-length relationship (Figure B.2). We assessed spawning probability based on the total number of marked individuals in each size class observed making a distinct spawning migration relative to the number of marked individuals in each size class detected during that year (Table B.2).

We estimated stage transition probabilities based on the proportion of marked survivors from a given stage during one year that grew into another stage in the following year in SFWWR and Mill Creek (MC; Table B.3a and B.3b). We also evaluated the range of growth rates for different sizes of bull trout from each of the populations of interest (Figure B.3)

We estimated survival rates for six stage of bull trout based on a Barker model implemented in Program MARK and analyzed with a random effects model in a Bayesian framework. We modeled survival as differing between years and among groups. We used minimally informative prior distributions on the mean (μ) and standard deviation (σ) of the hyperdistribution. We assumed a normal prior distribution on μ , with a mean of 0 and standard deviation (SD) of 100, and a gamma distribution prior for σ , with $\alpha = 1.001$ and $\beta = 0.0001$. For all other parameters (not included in the hyperdistribution), we assumed a reasonably uninformative prior distribution of with a mean of 0 and SD of 1.75 (White et al. 2009). We ran 10 complete Monte Carlo Markov Chains, and after assessing convergence of the chains, we used a sample size of 10,000 from the posterior distribution of a single chain to calculate summary statistics. For the stage-specific survival parameters in the population models, we back-transformed estimates of μ and σ from the posterior probability distribution to get the mean estimate of survival and 95% credible intervals. These values represent the mean estimates of survival for each life stage over ten years and the associated temporal process variance, with sampling variance removed (Table B.4).

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Table B.1. Size classes for bull trout, given in total length (TL) and fork length (FL), and the median length in each size class. Size classes approximate ages, based on data from a von Bertalanffy growth model and observed growth estimated from individuals marked and recaptured in the South Fork Walla Walla River, Oregon.

Size class	TL (mm)	FL (mm)	Median TL (mm)
1	60 to 120	65 to 115	95
2	120 to 180	115 to 175	150
3	180 to 240	175 to 230	210
4	240 to 300	230 to 290	270
5	300 to 360	290 to 345	330
6	360 to 420	345 to 405	390
7+	>420	>405	500

Table B.2. Total number of distinct spawning migrations of marked bull trout in each life stage per year relative to the total number of marked fish in each life stage that were detected in that same year. The proportion of observed spawning migrations relative to the total number of fish detected was used to establish a baseline estimate of spawning probability for population models.

Year	Observed spawning migrations				Total marked fish detected			
	stage4	stage5	stage6	stage7+	stage4	stage5	stage6	stage7+
2003	0	1	0	14	3	7	6	20
2004	0	1	0	15	16	10	4	32
2005	1	4	0	13	14	16	7	19
2006	0	5	4	12	12	11	10	17
2007	1	1	4	9	12	7	5	15
2008	2	1	3	10	9	2	5	10
2009	0	2	1	8	3	3	2	7
2010	2	1	0	6	18	4	2	8
2011	4	2	1	11	27	5	3	10
Total	10	18	13	98	114	65	44	138
Proportion	0.09	0.28	0.30	0.71				

Table B.3. Number of recaptured individual bull trout from the (a) South Fork Walla Walla River and (b) Mill Creek populations that transitioned from one stage into another in the following year. Data shows for recaptures for all years between 2002 and 2011 combined. Size transition probabilities are shown in parentheses. For simplicity, some transition probabilities were combined in population models.

a.

Stage in year 2	Stage in year 1						
	1	2	3	4	5	6	7
1	2 (0.05)	--	--	--	--	--	--
2	36 (0.95)	3 (0.08)	--	--	--	--	--
3	--	23 (0.64)	2 (0.12)	--	--	--	--
4	--	10 (0.28)	14 (0.88)	4 (0.30)	--	--	--
5	--	--	--	8 (0.62)	4 (0.67)	--	--
6	--	--	--	1 (0.08)	2 (0.33)	8 (0.8)	--
7	--	--	--	--	--	2 (0.2)	10 (1.0)
TOTAL	38	36	16	13	6	10	10

b.

Stage in year 2	Stage in year 1						
	1	2	3	4	5	6	7
1	--	--	--	--	--	--	--
2	--	6 (0.46)	1 (0.17)	--	--	--	--
3	--	3 (0.23)	0 (0.00)	--	--	--	--
4	--	4 (0.31)	4 (0.66)	--	--	--	--
5	--	--	1 (0.17)	--	2 (0.11)	--	--
6	--	--	--	--	15 (0.83)	18 (0.24)	--
7	--	--	--	--	1 (0.06)	58 (0.76)	133 (1)
TOTAL	0	13	6	0	18	76	133

Table B.4. Estimated mean (μ) and standard deviation (σ) of the hyperdistribution for survival rates. The mean and 95% credible intervals for μ and the mean of σ from the posterior distribution are reported.

Life stage	Survival (μ)	5% CI	95% CI	SD (σ)
Stage 2	0.264	0.154	0.403	0.205
Stage 3	0.382	0.258	0.539	0.097
Stage 4	0.384	0.194	0.608	0.165
Stage 5	0.389	0.311	0.527	0.048
Stage 6	0.444	0.318	0.586	0.076
Stage 7	0.471	0.293	0.666	0.189

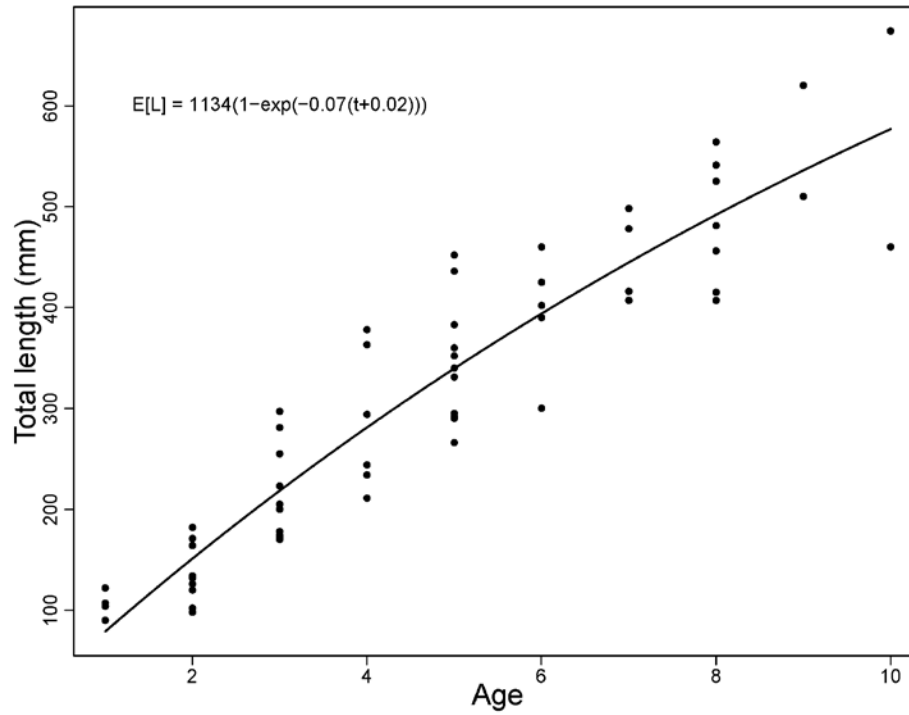


Figure B.1. Von Bertalanffy growth curve based on aged otoliths removed from 62 sacrificed bull trout from the South Fork Walla Walla River, Oregon, between 2002 and 2011. The growth equation is shown on the graph.

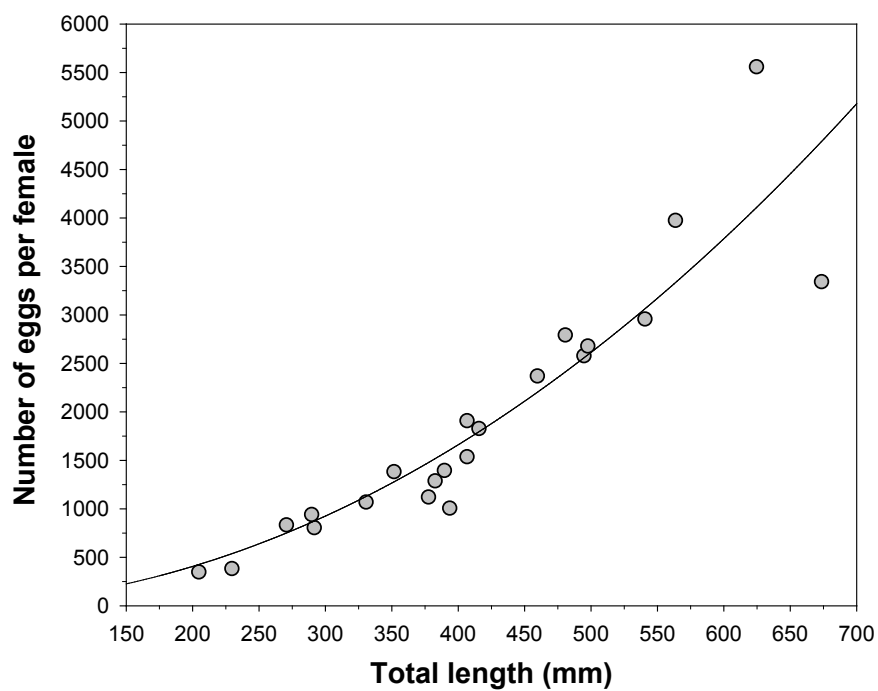


Figure B.2. The total number of eggs from female bull trout of a given total length (mm). Data were from sacrificed or incidentally taken bull trout in the South Fork of the Walla Walla River, Oregon, between 2002 and 2011.

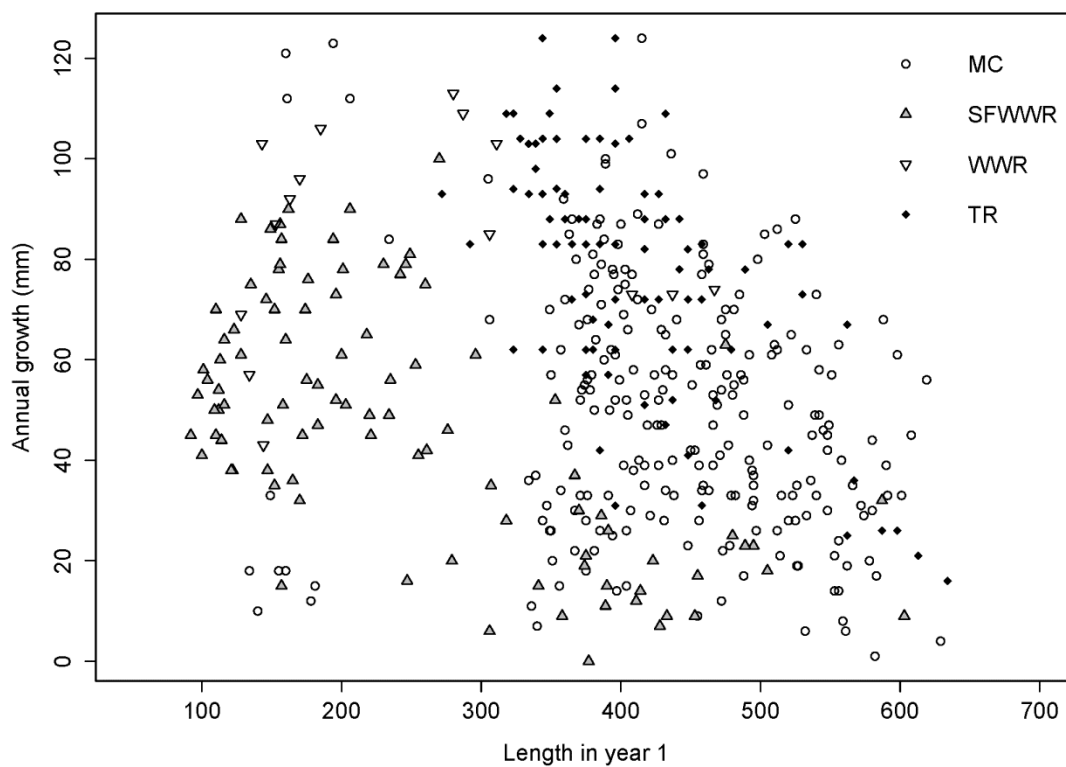


Figure B.3. Annual growth rate (mm) for bull trout across a range of initial lengths from the mainstem Walla Walla River (WWR) and three tributary populations: Mill Creek (MC), South Fork Walla Walla River (SFWWR), and Touchet River (TR).

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Dear Howard Schaller,

I am in the process of preparing my dissertation in the Department of Watershed Sciences at Utah State University. I hope to complete this degree in the Spring of 2013.

I am requesting your permission to include our coauthored paper, Implications of Life-History Variability and Metapopulation Structure for Bull Trout Population Persistence, in my Ph.D. dissertation, as per graduate school requirements. As discussed previously, I will also submit our manuscript to Ecological Monographs or a similar journal upon completing my degree. You will be cited as a co-author on the title page. Please advise me of any changes you require.

Please indicate your approval of this request by signing in the space provided. By signing this letter, you acknowledge that the work leading to the completed paper was primarily my own. Please contact me with any questions.

Thank you for your cooperation,
Tracy Bowerman

I hereby give permission to Tracy E. Bowerman to reprint the following material in her Ph.D. dissertation.

Chapter to be published as Bowerman, T.E., P. Budy and H.A. Schaller.
Implications of Life-History Variability and Metapopulation Structure for Bull Trout Population Persistence, to be submitted to Ecological Monographs.



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- Created a metapopulation model to investigate how multiple, connected populations might respond to climatic and anthropogenic environmental changes.
- Designed and implemented field experiments to assess egg-to-fry survival, condition, and timing of fry emergence in relation to abiotic variables within the hyporheic zone.
- Supervised field crews, managed large data sets, wrote annual reports, compiled and analysed data using numerous analytical approaches, including capture-mark-recapture methods, univariate and multivariate analysis, generalized linear models, mixed effects models, and matrix population modelling.

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- Collaborated with diverse stakeholders and government agencies to implement conservation initiatives and pass federal legislation regarding riparian and aquatic monitoring programs and wilderness designation.
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- Collected observational data on geophagy behavior in twelve species of parrots.
- Assessed factors affecting nesting success of macaws.
- Analysed large data sets, trained and managed field crews, and presented research to public.

Entomology Intern, USGS BRD, Kilauea Field Station, Volcano, Hawaii*Supervisor: Dr. Peter Oboyski**January-April 2001*

- Collected field data and performed laboratory experiments to determine rates of wasp parasitism on native moth species.
- Analysed spatial distribution and rate of invasion of non-native insects across Hawaii.
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Bowerman, T. and P. Budy. 2012. Incorporating movement patterns to improve survival estimates for juvenile bull trout. *North American Journal of Fisheries Management* 32(6): 1123-1136.

Bowerman, W.J., P. Johnson, **T. Bowerman**. 2010. Sublethal predators and their injured prey: Linking aquatic predators and severe limb abnormalities in amphibians. *Ecology* 91(1): 242-251.

Al-Chokhachy, R., B. Roper, **T. Bowerman**, P. Budy. 2010. A review of bull trout habitat associations and exploratory analyses of patterns across the interior Columbia River Basin. *North American Journal of Fisheries Management* 30(2): 464-480.

In preparation

Bowerman, T., P. Budy, and H. Schaller. *In preparation*. Conservation implications of multiple life-history strategies and metapopulation structure for a stream-dwelling char, bull trout.

Bowerman, T., P. Budy, and B. Neilson. *In preparation*. Effects of fine sediment, hydraulic conductivity, and hydraulic gradient on survival and development of bull trout embryos.

Bowerman, T., B. Neilson, J. Heavalin. *In preparation*. Evaluation of vertical hydraulic flux through the egg pocket of bull trout redds and implications for embryo survival.

Technical reports

Budy, P., D. Epstein, **T. Bowerman**, and G.P. Thiede. 2012. Bull trout population assessment in northeastern Oregon: A template for recovery planning. 2011 Draft Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2012 (*Draft*): 1-77.

Budy, P., L. Tennant, **T. Bowerman**, and G.P. Thiede. 2011. Bull trout population assessment in northeastern Oregon: A template for recovery planning. 2010 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2011 (5): 1-90.

Budy, P., **T. Bowerman**, and G.P. Thiede. 2010. Bull trout population assessment in northeastern Oregon: A template for recovery planning. 2009 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2010 (3):1-48.

Budy, P., P.D. MacKinnon, **T. Bowerman**, and G.P. Thiede. 2009. Bull trout population assessment in northeastern Oregon: A template for recovery planning. 2008 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2009 (1): 1-57.

Budy, P., P.D. MacKinnon, **T. Bowerman**, and G.P. Thiede. 2008. Bull trout population assessment in northeastern Oregon: A template for recovery planning. 2007 Annual Progress Report to US Fish and Wildlife Service. UTCFWRU 2008 (4): 1-62.

PRESENTATIONS

Bowerman, T., P. Budy. 2012. A multi-scale investigation of factors limiting bull trout viability. U.S. Fish and Wildlife Service Columbia River Fisheries Program Office, Vancouver, WA. *April 19, 2012.*

Bowerman, T., P. Budy, and B.T. Neilson. 2011. Effects of substrate size, hyporheic flow, and spawning site selection on bull trout egg and alevin survival. Presentation, American Fisheries Society annual meeting, Seattle, Washington, *September 5-8, 2011.*

Bowerman, T. and P. Budy. 2010. How do habitat connectivity and dispersal rates affect population dynamics of an imperiled freshwater fish? Poster, Society for Conservation Biology, International Annual Meeting, Edmonton, Alberta, Canada. *July 4-7, 2010.*

Bowerman, T., P. Budy, R. Al-Chokhachy, and H. Schaller. 2010. Patterns of bull trout movement and life history expression: What can we learn from multiple years and multiple sites using passive PIT-tag antennas? Presentation, American Fisheries Society, Western Division Annual Meeting, Salt Lake City, Utah. *April 20-23, 2010.*

Bowerman, T. and P. Budy. 2009. River engineers: Do spawning fish alter small-scale stream hydraulics? Presentation, Ecological Society of America, Annual Meeting, Albuquerque, New Mexico, *August 6, 2009.*

Bowerman, T.E., P.E. Budy, H.A. Schaller. 2008. Use of predictive models to assess the importance of riverscape connectivity on the distribution of an imperiled fish species. Presentation, American Fisheries Society Western Division Annual Meeting, Portland, Oregon. *May 5, 2008.*

AWARDS AND GRANTS

Student presentation and travel award (\$500).	<i>2011</i>
Western Division American Fisheries Society.	

Student presentation and travel award (\$700).	<i>2010</i>
Strategic Environmental Research and Development Program (SERDP) to attend the Society of Conservation Biology Annual International Meeting, Edmonton, Alberta.	

Utah State University graduate student travel award (\$500).	<i>2009</i>
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Teaching Assistant of the Year award (\$250).	<i>2009</i>
College of Natural Resources, Utah State University.	

Seely-Hinckley Scholarship, Utah State University (\$4,500). 2008

Vice-presidential Fellowship, Graduate School, Utah State University (\$15,000). 2007

Stepping up to leadership: Training and development for environmental leaders. 2006
Presented by Training Resources for the Environmental Community (\$3,000).

TECHNICAL AND RESEARCH SKILLS

- Computer programs: Microsoft Office suite, SAS, R, Program MARK, RMARK, Program Distance, RAMASmetapop, ArcGIS, Access database including SQL, Matlab.
- Population assessment techniques: estimation of individual traits and demographic rates including abundance, survival, growth, and phenology; capture and transition probabilities; occupancy modelling; population trends; matrix modelling; population viability analysis.
- Analysis of fisheries data: stock-recruitment dynamics, age and growth, mortality, relative abundance, CPUE, condition, diet, bioenergetics, movement assessment, community indices, species interactions, habitat evaluation.
- Hydraulic, hydrologic, and geomorphologic methods: Channel and bed surveying, sediment sampling, particle size analysis, hyporheic flow rates, (vertical hydraulic gradient and hydraulic conductivity), hydraulic modelling using HECRAS, iRIC, and PHABSIM.
- Fisheries and aquatic community sampling techniques: electrofishing, gill-netting, gastric lavage, implanting PIT tags, snorkel counts, aquatic macroinvertebrate sampling.
- Experience capturing, handling, and marking a variety of different taxa, including birds, terrestrial mammals, bats, amphibians, and fish.
- Certifications: Wilderness First Responder, Avalanche Rescue I, Swiftwater Rescue.
- Proficient in written and spoken languages: German and Spanish.

PROFESSIONAL SERVICE AND AFFILIATION

Reviewer for *Ecology*, *Conservation Biology*, *Oecologia*, *Ecology of Freshwater Fish*, *Journal of Fish Biology*, *Transactions of the American Fisheries Society*, and *North American Journal of Fisheries Management*.

Student member, American Fisheries Society. 2007-present

Student member, Ecological Society of America. *2009-present*

Student member, Society for Conservation Biology. *2010-present*

VOLUNTEER WORK

Board Member, Nordic United, Logan, Utah. *2010 – 2012*

Board Member, Upper Deschutes Watershed Council, Bend, Oregon. *2004- 2007*

Fundraiser, The Little Sister Fund, Kathmandu, Nepal. *2004- present*

REFERENCES

Phaedra Budy, Professor (Major professor)
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